PHYSIOLOGY OF THE NERVOUS SYSTEM

PHYSIOLOGY OF THE NERVOUS SYSTEM

BY J. P. MORAT

of the University of Lyons

AUTHORISED ENGLISH EDITION

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Translator's Preface

THE present work forms the portion of the Treatise on Physiology by Profs. Morat and Doyon which is devoted to the Functions of Innervation.

In completing the English version of Professor Morat's well known work on the physiology of the nervous system, the translator expresses the hope that he has succeeded in interpreting the views of the author with fidelity and accuracy. It has been his aim to adhere as closely as possible to the text throughout the work, making use of paraphrase only when this was essential to clearness of expression.

The subject treated in the following pages is a most complicated one; but there can be no doubt that this volume embodies the latest advances in our knowledge of the nervous system and portrays the most recent views and ideas on this very intricate branch of physiology.

H. W. SYERS.

WIMPOLE STREET,
October, 1905.

Preface

In every living being a double current of matter and energy is present, running in a definite direction which never varies. In these two currents the transformations of energy accompany those of matter; they are sometimes united, sometimes separated, and their union is the starting point of a cycle of which their separation emphasizes the termination. This cycle is the simplified image of vital evolution; and in it the first traces of organization are sketched out. But in proportion as this cycle becomes complicated and elaborated we may observe the advent of fresh cycles more or less resembling it, which superpose themselves, interfere with and bestow upon it a new value. Innervation corresponds to a cycle of this nature.

In fact, while the material and energetic currents proceed from the ingesta to the excreta through the intestines and the vessels, a third and an incomparably weaker current, that of the nerves, finds for itself distinct and separate channels and intervenes for the regulation of the two former, ensuring for them their most effectual employment. The nervous system does not provide force, it utilizes it; and this duty devolves on it by reason of the perfection of its own organization. It is the nervous system which decides at what moment the energy accumulated by the living being shall be liberated, in other words shall leave matter and exert its motor functions. This point it decides with the assistance of information communicated by the organs of the senses, and by means of a sometimes extremely lengthy work of internal elaboration brought to bear on this information arriving from the exterior.

In short, by the disturbances entering into it the nervous system receives impressions from the external world of which it thus obtains knowledge; by its own activity it forms a judgment of all surrounding it from the point of view of utility; finally, it reveals this judgment by a motor act calculated to ensure the preservation of the organism. Such is the cycle of the nervous current; it implies successively an external phenomenon of impression, an internal phenomenon of sensation, another external phenomenon of motor response to the

impression, itself followed by another internal phenomenon of sensation registering the accomplished movement. In the nervous system all movement induces sensation, all sensation induces movement. This system amongst its most extraordinary attributes possesses a power of adjournment concerning the events depending on it. These events, which on a reduced scale and in a condition of representation or images, it constructs internally with the data furnished by the senses, it preserves until an appropriate moment arrives for partially realizing them in the form of external movements.

From the fact of the introduction of sensation into the cycle unrolled in the nervous system, events assume for it a particular signi ficance which otherwise they would not possess. According to the affective tonality (agreeable or painful) of the sensation, they are either favourable or the reverse. Obviously, and in spite of the errors which it may commit, the living being seeks the former and avoids the latter. Whether its activity is free to choose or whether it is enclosed in an inflexible determinism, is a problem which it is not the province of physiology to inquire into. But whether rigid or elastic this determinism includes a new element and factor, sensibility, which outside of the living being is either wanting, or at all events is not apparent.

The relations between cause and effect which elsewhere seem so simple are here on this account extremely complicated and modified. The power possessed by the living being, and more especially by the nervous system, of the internal preservation of external events by their reduction to the condition of representations and of their later realization and enlargement in the form of visible movements, conveys to us the false impression that the end and aim of an act is the cause of this act. The cause of an act cannot be in the future, but may be in the memory of a previous act of the same nature remembered as being either useful or hurtful and which on this account determines the direction given to the movement. There must always be an aim, a general or particular tendency determined by the sensory nature of the living being, but this aim is an effect and not a cause. The past always involves the future, but in this past the living being knows how to choose, and when it recreates it it does so as much as may be to its own advantage ; whence its almost indefinite degree of perfectibility.

Thus we can see that the study of physiology gives rise to, or at any rate borders on, problems which are not in any way its special province ; and for the rest demands from psychology solutions which the latter seeks for with the aid of its own methods. A kind of neutral area,

common to both sciences, exists which the former endeavours to appropriate by pushing farther back the boundaries separating it from the latter. Progress must inevitably be slow, as apart from the fact of this study bristling with difficulties of every kind, methods, in spite of the efforts of a host of inquirers, still remain crude and unsuited to the infinite delicacy of the organs of the nervous system and their component elements.

J. P. MORAT.

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Innervation

In the living being all the phenomena appertaining to crude matter are observable, but the converse does not hold good. It is obvious that a being endowed with life possesses characteristics and presents manifestations for which in dead matter we can find no parallel; and the most marked feature distinguishing the one from the other is that of *sensibility*. Here is brought before our notice a fact of a purely internal nature, eluding observation as it is generally understood in science, but which common sense constrains us to attribute to beings resembling ourselves, while at the same time denying it to all objects in which this resemblance cannot be discerned.

Sensibility and Energy.—This attribute, *sensibility*, cannot in the living being act as a substitute for the energetic phenomena of matter; it is merely superposed to these phenomena, and connected with them by a double reciprocal link. They preside over it in the sense that a subject gifted with feeling must, of necessity, require an object to be felt; and, on the other hand, sensibility exercises a control over these phenomena of energy, inasmuch as, though incapable of modifying them as a whole, it can still regulate and control them in their execution of functions directed towards an end of which the living being itself is conscious.—This reciprocal link not only controls the relations of the living being with all surrounding objects; it is also, and simultaneously, the distinctive feature of its organization. In its development, as much ontogenetical as phylogenetical, it is the living being which is at once both artificer and final cause.—From this double link, so frail in itself, and yet so intimate, proceeds the *unity* of beings endowed with life, and in this organism, where *each part depends on the whole, and the whole on each part*, a synthesis is effected which confers upon it its *individuality*. This prodigy of complexity is also a prodigy of unity.

Sensibility and Determinism.—A science having for aim the study of a being so constituted should never lose sight of this double character, and more especially when appealing to the methods and general principles of other sciences. Dissociated and brought back to the crude state of common matter, the primary elements constituting the living being reveal to us in their reactions the same inflexible constancy that charac-

terises the laws known as physico-chemical ; yet, associated in the individual, their grouping and organization display that infinite variety and contingency whence individuality is derived. How can this proceed from that ? How can that which is invisible in the element become apparent in the whole ? To these questions we can find no answer ; but, in science as elsewhere, it is always imprudent to run foul of the information given by common sense, and a problem is not solved when one of its terms has been omitted.

The mind, desirous of being logical, is in fact at first offended by this contrast, and endeavours to annihilate it by evading one of the two points of view. The rigid determinism of purely energetic sciences has been transported, without restriction or selection, into biological science. In the past, and even at the present time, physiology has overlooked, and still overlooks, the fact of the being which it studies possessing sensibility ; and has in every case refused to acknowledge this sensibility as a causal or conditioning influence in the determinism of vital phenomena. It has carefully arranged the balance-sheet of the forces of the organism, while taking no interest in the function which regulates their employment. As physical science finds no place for sensibility, neither has physiology accorded it one. The time seems to have arrived for a reaction against these exaggerations. In the living being, just as *movement depends on sensation, so does sensation depend on movement.*

In both cases the nature of the link is unknown to us ; but none the less does this link exist, and is in biology the foundation of all that distinguishes it from pure physics.

Sensibility and Organization.—In the living world sensation presents extremely varied degrees, and its development proceeds on a line parallel with that of the organization itself. It is only strongly marked in beings provided with the differentiated system known as the *nervous system ;* it increases in importance and elaboration with the progressive development (phylogenetical and ontogenetical) of this system. In such beings, of whom we ourselves form a class, a division of attributes is effected between the tissues, some of these employing the efficient energies which take part in the execution of organic actions, while another, the nervous tissue, watches over this employment, coordinating and regulating it. This latter is pre-eminently the sensory tissue, and is in a high degree both excitable and capable of causing excitation. It is this tissue which receives the stimulation and returns it, but transformed by the progress through its paths ; and again it is this tissue which ensures the reciprocal dependence and subordination of the elements to the whole and the whole to the elements, and so confers on the organism its individuality, its unity.

Excitability and Sensibility.—All living matter is excitable; or, to put it otherwise, it responds to actions directed against it, by an expenditure of the special energy which it constantly accumulates internally. This motor reaction is never hap-hazard, but—and this fact is demonstrated by experiment—is always directed with the definite aim of preservation of life in the susbtance stimulated. Excitability is therefore not merely a motor manifestation, but is duplicated by an internal fact of rudimentary consciousness. It should therefore be considered as either a degraded form or a first rough sketch of sensation. The elaborated organization of the superior animals, by giving to it its highest development, permits of our analysing the conditions of its existence; fundamentally these conditions are everywhere the same; they are located in the links of reciprocal dependence of the portions composing the organism. The more simple and homogeneous is the latter, so much the more do its reactions resemble those of ordinary movement, and so much the farther are they removed from those which characterize genuine sensibility. But in proportion as the organism is complex and differentiated, so much the more will its movements possess the contingent characteristics of sensible and intelligent beings.

Action and Reaction.—In other words, the living being reacts against actions reaching it from the external world, and in so doing obeys a general, universal, and indeed fundamental law, one of the first inscribed in the physical code, a law, obedience to which no living body in nature can escape. Only, from the fact of organization itself, this law has assumed a new character, of which it may be said that it implies in the living being a *remembrance of the past* and a *prevision of the future*. The more elevated is the organization, the more prominently does this character stand forth; on the other hand, the nearer we approach the purely physical elements entering as components into this organization, so much the more is this character effaced, nothing being left but the simple reaction strictly and solely answering to the action of the present moment. Vital reaction, practically so different from physical reaction, proceeds from it by successive halting places and elaborations, just as the living being itself is evolved from progressively organized crude matter.

Division.—The nerve tissue is, like all other tissues, originally formed of cells; but while other cellular structures are usually merely composed of duplicated and juxtaposed elements, it, thanks to the connexions established between its component parts, displays a genuine systemitization. Its study may therefore be carried on from two different points of view; one in which the functions common to all its elements are considered (*cellular functions*), the other, in which the functions

special to the groups or systems formed by these elements are taken into account (*systematic functions*). In the study of nerve tissue the distinction between these two orders of functions is a fundamental one, and the obscurity still enveloping numerous questions connected with this study is partly due to the fact of this distinction being so frequently ignored.

The first of these studies completes the history of the cellular functions arranged in unison with the principal types of living elements. The second permits of our penetration into the aggregate functions to which the mutual association of these elements gives rise, and it is in the nervous system that we shall find the connexion where these aggregations are brought into being and their functions organized. The study of the nervous system is a kind of nodal point in the exposition of physiological science.

PART I

Elementary Nervous Functions

THE complexity of the living being and of its smallest organs is such as to compel us to study them from two points of view: the one *static*, or that of absolute repose, that is to say, death; the other *dynamic*, or that of activity, that is to say, life, in its different manifestations. Anatomy is concerned with the static condition, taking account, as it does, of vital forms in their fixed state; the dynamic condition, or that which physiology investigates, is concerned with movement. The two sciences are mutually related and sometimes their special methods are interchanged. A summary review of the principles of the one always aids in the elucidation of those of the other. By mutually borrowing they tend to reciprocally fill up their lacunæ.

1. **Static Unit.**—A static unit of the nervous system exists which is commonly known by the name of element: this is the *neuron*. This unit is of cellular order and is indeed a *symbiosis*, in the sense that to the fundamental cell of which it consists others are added which in a way form one structure with it. It is an element in the relative sense of the term only, because a cell is a being of complex organization, but this unit is very well defined and thus acquires great importance. It is necessary therefore to briefly recapitulate its most essential characters.

2. **Dynamic Unit.**—Corresponding to this static unit there exists a dynamic unit in the same way as for the muscular element, the glandular element, etc. In the nerve this dynamic unit is less easily recognizable, because it does not declare itself, as do the preceding elements, through externally visible phenomena (contraction secretion), but only by the excitability which is more or less the heritage of every cell, or rather by the reaction of this excitability on that of the other tissues which are connected with the nerve.

This dynamic unit, which we can only describe by the unsatisfactory name of *elementary nervous irritability*, is the aggregation of the energies which take their origin in the neuron, in order to preserve its existence, its composition, its structure, its internal and external manifestations, the whole being co-ordinated to a definite end.

Organization of Energy.—Just as in the nervous element the structure is not homogeneous, but is made up of complicated structures which nevertheless form a coherent whole, so in this element, as in every cell, there is an organization of energy, which, by the dependence which it creates between its multiple forms, causes the latter to take part in the conservation of the element, and guarantees its social action in the economy. Like every living individuality, the nervous element, the neuron, is at the same time both single and multiple, and it must not be forgotten that it is so both from the dynamic and static point of view.

The Multiple Forms and Transformations of Energy in the Nerve.—If it be asked what is the energy which circulates in the nerve, the question is badly expressed, because it suggests that one sole force occupies its substance (as does electricity a conducting wire), and, *à priori*, it is obvious that such a comparison is inaccurate. The utmost that can be done is to investigate the nature of the final energy which the nerve makes use of at its point of contact with the muscles, or of the organs which it excites. But before arriving at this last phase, it is certain—for proofs thereof exist—that energy has undergone many transformations of which we only know those which are the most striking.

(*a*) *Chemical Force.*—In the nerve, as in every tissue, force is present in its chemical form ; because, as in every other tissue, it is constantly produced by exchanges with the blood through the vessels which irrigate it (gaseous exchanges and those of soluble substances).

(*b*) *Caloric Force.*—In masses of nerve tissue of considerable size it is now admitted that there is a slight disengagement of heat ; because the temperature of these masses may be slightly higher than that of the blood which circulates in them (Mosso).

(*c*) *Electric Force.*—In the nerve, as in all the elements having a definite orientation, electro-motor phenomena have been discovered which give rise to currents passing in a definite direction ; so that a place must be given also to electricity in the transformations of the energy employed by the nervous element. It is only necessary to be aware that the assimilation of a nerve to an ordinary electric conductor is radically inaccurate. The conception of these currents is complicated and one, so to say, special to the nerve, and their circulation probably takes place in particles in size approaching that of the molecule.

Cycles of Energy.—Those chief forms of force which arise by transformation the one from the other enter into cycles of energy, which sketch the first outlines of that organization of force in the element, without which all would be confusion, and, thanks to which, order and unity become paramount in it.

We are but imperfectly acquainted with the detail of these cycles ; but everything shows that in the nerve element (as in every cell) they are numerous, giving rise to varieties and infinite gradations. But that which chiefly characterizes them, in the living being, is their mutual penetration, their superposition.

their convergence towards a definite end. Not one is absolutely complete in itself; but each on the contrary expends a part of its force on neighbouring cycles, both parallel and successive. Hence it is that insurmountable difficulties often arise in the analysis which endeavours to isolate them in order more accurately to study them.

Functions.—The cycles of energy which are essentially simple, and are concerned with the performance of what we call nerve functions, are what form the foundation of that dynamic nervous unity which our intelligence is not yet accustomed either to see or to investigate, but which in our science is just as necessary as the cellular conception (which is the concrete form thereof) is in anatomy. If the details of this organization of forces were better known it would lead us without transition to the knowledge of those complex acts which are the functions and which we at present only recognize through their results.

Their Double Nature.—These functions are in a nervous element (as in every living element), of two orders; both make use of the energy which penetrates the nerve and quits it after transformation; but from it they evolve a different order of result. Some are concerned with organization and, when once this is established, the conservation of the organization of the neuron: for this reason they are called *organotrophic;* they are *internal* to the neuron itself. The others affect the social aspect of the cellular individuality so far as this concerns the total nervous system and the individual itself: hence these functions are those properly called *nervous;* they are external to the neuron, and while the first establish connexion between its constituent parts in order to preserve its static and dynamic identity in the midst of perpetual renewal of its substance and its energy, the second form amongst all the neurons (and the elements in connexion with the neuron) a systematized tie which gives unity to the nervous system, and hence to the individual of whom it forms a part.

Their Reciprocal Dependence.—The internal and external functions of the neuron, both trophic and nervous, however well defined they may be in their object, have necessarily very close mutual inter-relations. The second are clearly not possible unless the first are in existence; the functional activity of an element, whatever it may be, presupposes its nutrition: but in their turn, the first assume with regard to the second a more indirect dependence, but one which is equally real; nutrition languishes when function is in abeyance.

CHAPTER I

THE NERVOUS ELEMENT

THE nervous element is the neuron. The neuron is essentially a cell which is differentiated for the performance of a special function, that, namely, of innervation or of stimulation of other cellular elements. This cell (*the nerve cell*) is provided with prolongations (nerve fibres) which proceed to a greater or lesser distance, but have a free termination, so that the structure is limited in a definite manner. To the nerve cell thus furnished with its prolongations other structures are superadded, and these are of a more or less cellular nature and origin (myelin sheath, and the sheath of Schwann with its nuclei). It is this cellular *symbiosis*, regarded in its totality, which forms the neuron.

A.—STATIC CONDITION OF THE NEURON ; ANATOMICAL DATA

1. **External Characters ; Dimensions.**—The dimensions of the neuron are very various, especially as regards length. Some are of microscopic dimensions (for example, in the retina) ; others may (in man) attain and even exceed a metre in length (for example, the nerves of the posterior root, going from the sole of the foot to the medulla oblongata) ; between these extreme dimensions many intermediate lengths may be found.

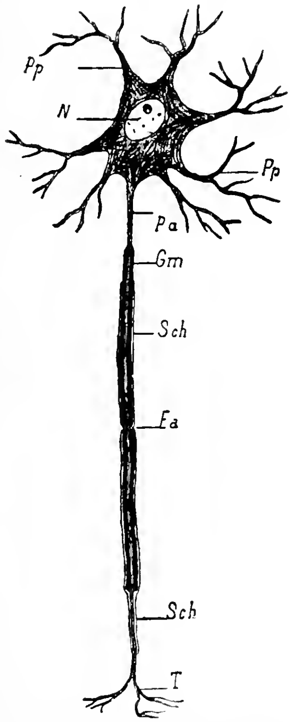


Fig. 1.—Diagrammatic representation of an ordinary neuron.

N, nucleus of the nerve cell ; *Pp*, protoplasmic prolongations ; *Pa*, axis cylinder ; *Gm*, sheath of myelin ; *Sch*, sheath of Schwann ; *Ea*, annular node ; *T*, terminal ramifications of the axis cylinder.

Form.—Not only the dimensions, but also the shape of neurons may vary extremely. These variations are in relation, both the one and the other, with the particular connexions which it is the duty of these elements to establish between the nervous system and the organs, as also between the different parts of the nervous system itself. Nevertheless, in spite of this apparent diversity, they may be brought back to a common type in connexion with their most general function.

General Type.—The neuron presents a swollen portion, which is its cell of origin (formerly known as, and still often called, the *nerve cell*) from which prolongations in different directions are given off. These prolongations are of two species : the first called *protoplasmic*, ramified considerably, without, however, anastomosing with one other ; the second, thinner and paler, called the prolongation of Deiters, or *axis cylinder*, proceeds to a variable distance from the cell origin and gives off branches, partly on its course (*collateral branches*), and partly at its termination (*terminal branches*). A tree with its roots, its trunk and its branches would thus sufficiently clearly depict this arrangement if there were added to it at the point of expansion of the roots, a swollen portion which would represent the body of the cell.

Signification of the parts.—From the physiological point of view the feltwork of the roots and the foliage of this miniature tree give rise in

the neuron to two parts which are functionally opposed, and which are united by the stem. The feltwork is, taken as a whole, an organ for the reception of impulses; the branches would form an organ for the distribution or rearrangement of these same impulses to the nervous or non-nervous organs in which they ramify. The trunk gathers them together and transmits them from one of its extremities to the other. As regards the cell, we shall endeavour to define the part which it plays a little farther on.

Synonomy.—In the new terminology the prolongations of the neuron formerly known as protoplasmic are called *dendrites;* the prolongation of Deiters, or the axis cylinder, is known as the *axon* or *neurite.* The axon is nothing more than a nerve fibre, of the same kind as those which form the peripheral nerves. Its essential portion is the axis cylinder, around which are placed the *myelin sheath,* then the sheath of Schwann, with its nuclei and its regularly arranged nodes.

From its initial to its terminal extremity the neuron thus presents three morphologically distinct parts, namely:—1, the *dendrites* or *protoplasmic prolongations;* 2, the *body of the cell,* formerly known as the nerve cell; 3, *the axon* or *neurite,* which is the axis cylinder covered with its double protective sheath.

(a) *Axon.*—Ranvier has shown the cellular nature of the envelopes of the axon. The myelin sheath is interrupted from point to point by the nodes of the sheath of Schwann, which divide it into regular *segments* (about a millimetre long in ordinary nerves) of which each bears a nucleus in the middle of its length. With its myelin contents (phosphorised fat), each segment would be comparable to a fat cell of cylindrical form, crossed in its axis by the prolongation of the nerve cell which is rightly known as the axis cylinder.

FIG. 2.—Interannular segment of the axon. *Ca,* axis cylinder; *n,* nucleus of the sheath of Schwann; *p,* protoplasm of the same; *e,* node of Ranvier.

Inasmuch as *after death* coloured or penetrating substances pass into the axis cylinder by the nodes, it has been thought that this was the normal route for the passage of nutritive material *during life.* But this idea is based on an inexact appreciation of the nutrition of cells, as it represents the cell as merely absorbing certain substances through the most delicate portion of its structure. Absorption, or, to speak more accurately, the metabolic exchange, is effected all over the surface, as is the case in every cell whatever. On the other hand, these exchanges

imply successive and numerous operations, mutations and transformations, in which the cellular contents (in this case myelin) take a part just as do all the rest.

The functions of the sheath of Schwann and of the myelin are often considered to be purely mechanical, or as comparable to those of an electric insulating substance. Without denying the part which the myelin plays in this connexion, it is certain that the principal functions of the cells which envelop the axon are not limited to so simple a rôle. These functions have essentially for their foundation a chemical evolution, which we can enounce in principle, but which our actual means do not permit us to accurately define.

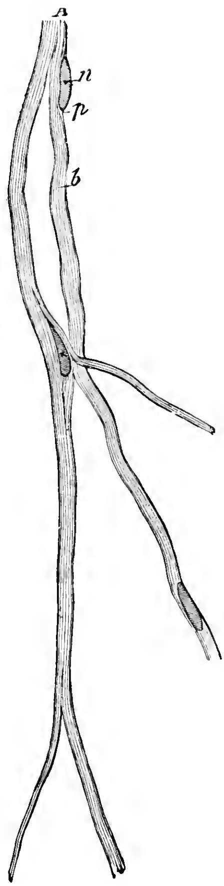


FIG. 3.—Non-myelinated fibres, or those of Remak.

n, nucleus; *p*, protoplasm surrounding it; *b*, constituent fibril.

Myelinated and non-myelinated fibres.—Near the termination of the axis cylinder, the myelin ceases at the level of a last node, which is called *preterminal*. The axis cylinder is thereafter bare. This portion deemed denuded is present in all nerves. In the nerves of the life of relation it is extremely reduced; in the branches of the great sympathetic it is sometimes of great length. These *non-myelinated fibres*, still called fibres of *Remak*, nevertheless do not form, as is obvious, a particular and independent species, but only the continuation of the *myelinated* fibres.

In the locality where it quits the nerve cell (prolongation of Deiters), the axis cylinder is equally denuded for a certain length. The cell itself is enclosed in a capsule, whose cellular nature has long been recognized. In the spinal ganglia of the frog, yellowish drops are found in the winter season, representing stores of fat (and not of myelin), forming a season's reserve, which disappears at the approach of summer (Morat). These stores belong to the cells of the pericellular capsule (Bonne). Although of a different nature, they have some analogy with the myelin reserve (this being permanent) of the peri-axile cells of the axon.

Segmentary Cells; Their origin.—The axis cylinder, which is uncovered at its two extremities, is thus bare throughout the whole of its length when first developed. It starts from the nerve cell, like a lengthening branch, until it attains the organ for which it is destined (Rouget and Kölliker). Mesenchymatous cells (cells of conjunctive nature) are arranged from point to point along its length, and mould themselves on it (Vignal). In their mode of appearance and their development they follow the same order as does the axis cylinder in its growth; that is to say, they extend from the proximal to the distal end of the axon. In their interior they secrete myelin, and thus become the segmentary cells of Ranvier. In the extra-rachidian, or peripheral, nerves they become invested with membranes which, being continuous, form the sheath of Schwann. In the deeply situated nerves of the spinal cord and of the brain, this sheath is wanting, and the myelin is limited externally by the protoplasm of the investing cells.

Collaterals.—The axon or neurite exhausts itself by ramifying in the organs, nervous or other, to which it transmits the impulse; but in its transit it frequently gives off fine fibres, which are very appropriately called collaterals. It is frequently the case that these fibres are not distributed along the length of the axon in a regular manner, but leave it only when it passes through some portion of grey matter, as the fibres of the great sympathetic in the ganglia, or those of the pyramidal tract in the pons. Thus these collaterals belong to the transmitting polar field, to which they give a particular extension and a special aspect, not coinciding with what was formerly supposed to hold concerning the relations between the nervous elements. All cells which are at a great distance from the nerve cell

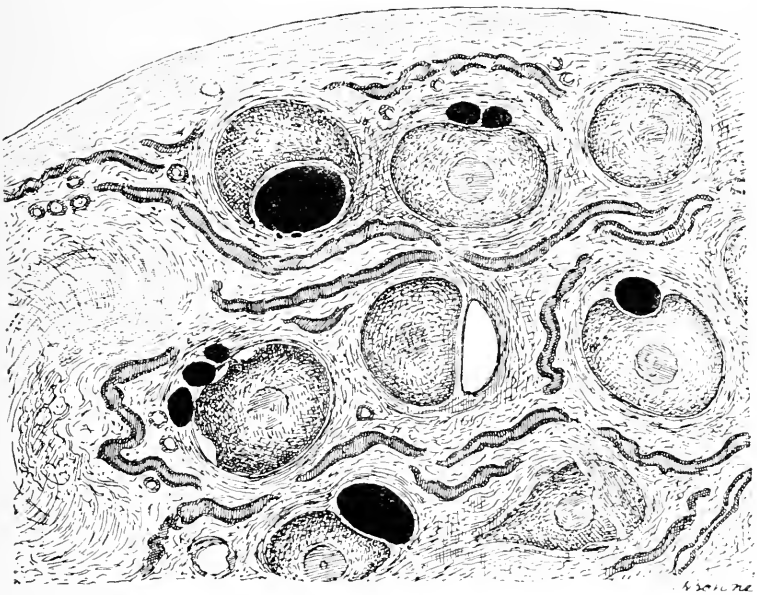


FIG. 4.—Season's reserve of the cells of the spinal ganglia of the frog in winter. Drops of fat, single or multiple, coloured by osmic acid, are seen in the capsule of the cell, and stand out more or less prominently in its interior. In the centre of the diagram a drop has been displaced by the manipulations, and the resulting empty space is seen in the capsule (from a drawing by Bonne).

are considered as fulfilling the same function as the strictly terminal ramifications; but there are some which take origin from the axon, sometimes at a short distance from the cell itself, almost at the origin of this axon. There has been hesitation in giving to these collaterals the same signification as the terminal branches of the neuron, and many hypotheses have been brought forward concerning these singular formations. And at first sight it seems indeed strange that the nerve element, which has just received the impulse by its dendrites in some area of grey substance, should there and then distribute it to this same field before leaving it. But if we reflect that in this field itself associating cells exist (cells whose dimensions are relatively limited, and which do not leave its territory), which transport to it in this way an impulse from a short distance, the fact will appear to us less surprising. Neurons of great length, as the radicular neurons of the anterior horns of the spinal cord, alone combine the function of associating cells with that of elements of projection. Of the impulse which it has just received from its dendrites, the neuron thus built up yields a portion to the dendrites of neighbouring neurons, while it carries away the remainder to

a long distance. It may be supposed on the other hand that these collaterals, if neighbours of the nerve cell, perform the function of dendrites, and belong to the receiving pole ; but although up to the present time no method of settling the question experimentally has been discovered, the resemblance of the collaterals to the terminal ramifications makes us inclined to support the first explanation ; the analogy of form, in the absence of the experimental proof, prejudices in favour of the analogy of function.

(b) *Body of the Cell.*—The body of the nerve cell presents itself in the form of a protoplasmic mass provided with a large nucleolated nucleus. In the interior of this mass the details of its structure can be made out. There may be distinguished in it a substance which is known as *chromatic*, which can be coloured by methylene blue, and a non-chromatic substance which is known as the *enchyleme*.

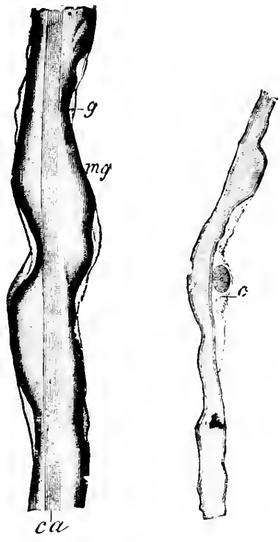


Fig. 5.—Nerve tubes (axons) of the spinal cord without the sheath of Schwann.

mg, myelin sheath ; *g*, peripheral envelope ; *c*, nucleus and protoplasm observable on the surface of some slender nerve tubes.

Fig. 6.—Neuroglia cells in a human foetus.

A, superficial cell of the neuroglia ; *B*, neuroglia cell of the grey matter.

The chromatic substance is looked upon as a sort of nutritive reserve, distributed in the cell in the form of grains, and visible even at the point of origin of the protoplasmic arborizations. It is this substance which changes its appearance, its distribution and its quantity, in the principal conditions of the cell, as the result of long continued stimulation or after section of the axon.

Golgi, Verrati and Nelis have demonstrated in the interior of the cell a network which would seem indeed to be double, occurring in two different planes, the one intracellular and the other pericellular. Bethe, and Apathy have also described networks of this description in the nerve cells of invertebrates. The connexions of these networks have not yet been definitely determined. The latter authors describe them as continuous with the constituent fibres of the axon. On the other hand, the body of the cell (and not only the dendrites) receive the contact of the terminal fibres of the neurons which enter into relation with them ; it may be that the pericellular network serves to establish these relations.

Cellulipetal and Cellulifugal Prolongations.—The body of the cell displays, in the neuron, a locality towards which the currents transporting the impulse tend to converge and to condense ; after this, according to the direction of the axon,

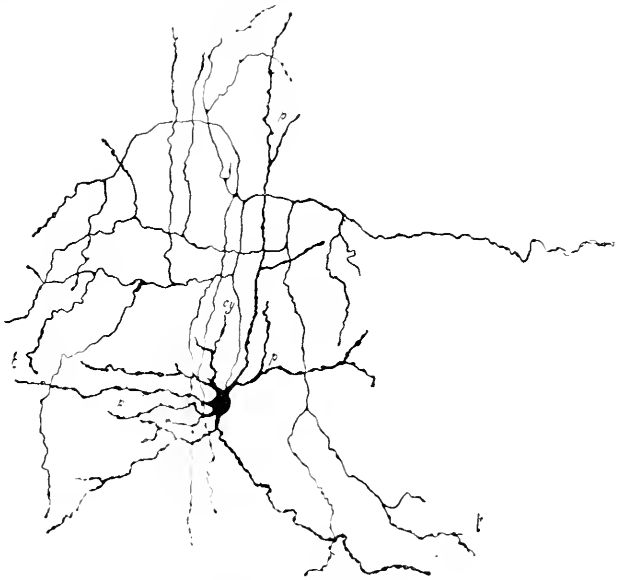


FIG. 7.—Short neuron of the cerebral cortex with its dendrites (varicose), its axis-cylinder prolongation (very fine) and the collaterals of the latter.

cy, axis-cylinder prolongation and its collaterals ; *t*, terminal varicose ramifications ; *p*, protoplasmic prolongations.

they begin to start again, diverging by the collaterals, which take their origin from the axon, sometimes but a short distance from the cell. Having respect to the progress of the impulse, the name of *cellulipetal* has been given to the converging prolongations and to the currents which they convey, and that of *cellulifugal* to those which proceed from the cell, and in this way diverge. When these two terms are considered as being equivalent to *centripetal* and *centrifugal*, the cell is compared to a centre of association of the neurons and of the transformation of the impulse.

As a matter of fact, the association really takes place at the reunion of the terminations of the axons with the origin of the dendrites ; the transformation of the impulse can only be possible at the identical place where this association occurs.

(c) *Dendrites.*—It would seem that the dendrites are the extended and ramified body of the cell, assuming the form of arborescent prolongations. It is only since the application of the method of Golgi that their real form has been recognized, and that it has been possible to ex-

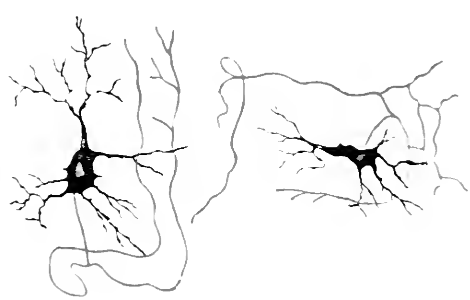


FIG. 8.—Short neuron with its two orders of prolongations seen as a whole.

The cellulipetal prolongations (protoplasmic) as well as the cells are in black ; the cellulifugal prolongations (axon and its collaterals) are in red.

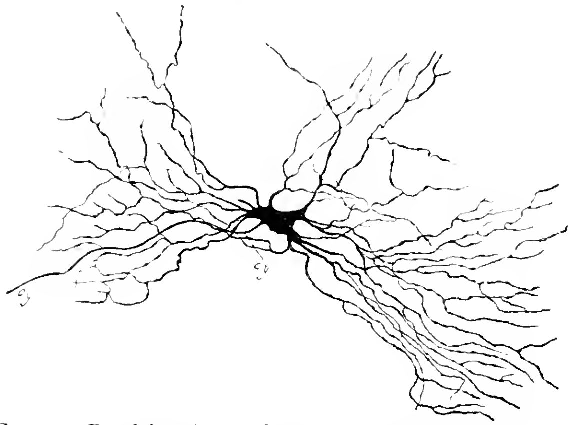


Fig. 9.—Dendrites (protoplasmic prolongations) of a root cell of the anterior horn of the spinal cord.

cy, its axis cylinder (prolongation of Deiters) proceeds to form the axon, which extends the whole length of the motor nerve.

plain their extension, often very considerable, throughout the grey matter, and even sometimes the white The peculiar appear- bordering matter. ance of these prolongations had formerly caused them to be considered as possessing a protoplasmic nature analogous to that of the body of the cell, and a function, rather trophic than nervous, in the exchanges between this latter and its surrounding medium. But their function as organs which are receptive and conductive of the impulse can no longer be contested.

However, their functional is not *à priori* exclusive of their trophic rôle ; it is only necessary that this latter be effected in a slightly different manner to that which was formerly current. It is scarcely admissible, as Golgi thought, that these prolongations act as conducting channels of the juices which they take up by their extremities in contact with vessels towards the cell ; but it is credible that the differentiated protoplasm, the conductor of the impulses, which is present in them. is steeped (here as elsewhere) in a *gangue* of primitive ordinarily trophic protoplasm, which, by its exchanges with the medium in which it is immersed, maintains its composition and its structure, and therefore its nervous function. Hence it may be asked if the modifications of form which ensue in these prolongations as the result of different conditions (stimulation, repose, fatigue), are anything more than the changes correlative to the nutritional requirements of these parts.

The Neuron and its Different Constituent Segments.
(*Succession, Different and Synonymous Forms.*)

Receptive Pole.	Protoplasmic prolongations. — *Dendrites.*	Nerve cell. — Body of cell with nucleus and nucleolus. — *Neurite.*	Prolongation of Deiters continued by the axis cylinder with its sheaths of myelin and of Schwann. — *Axon* or *Neuraxon.* *Monaxon* (single axon) *Inaxon* (long axon). *Dendraxon* (short axon). *Diaxon* (double axon). *Polyaxon* (multiple axon). *Schizaxon* (divided axon).	*Terminal* arborizations (at the extremity of the axon. *Collaterals* on the course of the axon. — *Telodendron.*	Emissive Pole.

2. Dynamic Polarization.—By this term is described the functional opposition which is attributed to the two extremities of the neuron. When applied to the neuron, the term dynamic polarization expresses a principle which is established by all experiments to which the nervous system is submitted; namely, that the waves of the impulse which pass through it traverse it in a definite direction, which is invariable. Thus the neuron has two poles; the one *receptive*, whose duty it is to receive the impulse; the other *distributive* or *emissive*, which transmits it to other organs, or to neurons other than itself. Between the two poles is an axial portion, the axon, which carries the impulse from one pole to the other. It is possible that the axial part possesses the power of propagating the impulse in either direction, but the poles themselves are incapable of inverting or exchanging their function.

There would be no inconvenience, and it would probably be advantageous, to describe, as Brissaud has suggested, the receptive pole as the *positive pole* and the emissive pole as the *negative pole*, it being understood that to these expressions, borrowed from the science of electricity, only a comparative signification, and in no sense that of identity, be ascribed.

As has been described above, each of these poles possesses ramifications which are frequently numerous and sometimes very widely extended. Both ramify in a territory or area whose size varies and in which each, according to its nature, receives or distributes the impulse.

In a given neuron when examined microscopically it is generally possible to say which of the two poles is the subject of examination. The receptive pole is that whose ramifications closely approximate the cell, so closely indeed that they appear to originate in the latter. The respective designation of the poles is not inferred from a structure which would explain their function, but is based on experimental observations which in a large number of cases have shown that the *propagation of the impulse proceeds from the dendrites to the axon, and passes through the cell body, and not inversely.*

The Experimental basis of the Polarity of the neurons.—The functional polarity of the nervous elements has been proved to demonstration by physiology. It lays down in principle that in each of these elements, possessing normal connexions, the impulse is transmitted in a definite direction, invariably the same, and that it neither returns nor oscillates, and this physiology proves in a very considerable number of such cases. And, on its part, anatomy having succeeded in defining in a number of instances the structure and the limits of these elements, it has been possible to establish certain relations between these anatomical data and the direction of the physiological conduction.

Generalization of this datum.—A neuron being given (or even a recognizable fraction of this element), it is usually possible to say in which direction the current of excitation is transmitted; but there are also cases in which it is impossible to predicate anything on this point. This is because the morphology of the neuron (form and situation of the cell and of its prolongation) is not in any way determinate, but, on the other hand, lends itself to the thousand exigencies which the reception and distribution of impulses require according to the order and the special nature of these functions.

Uncertainty in certain cases.—Whenever the neuron in which the problem of the direction of the conduction arises resembles those in which this direction has been ascertained by direct experiment, the reply is relatively easy; it becomes uncertain whenever this criterion is wanting; further, it may be only partial, that is to say, possible as

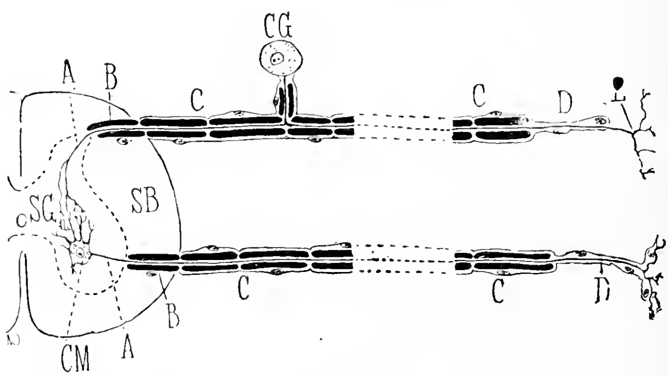


FIG. 10.—Comparison of the neurons of the posterior roots with those of the anterior roots (after M. Duval).

CM and CG, their cells of origin, one in the spinal cord, the other in the spinal ganglion; A, bare axis cylinder; B, portion of the same covered with a sheath of myelin without a sheath of Schwann; C, portion covered with a myelin sheath and sheath of Schwann; D, portion with a sheath of Schwann without myelin; E, bare terminal arborizations.

According to Dogiel, the cell CG of the spinal ganglion bears protoplasmic prolongations or dendrites analogous (though less visible) to those of the cell CM.

regards certain of the prolongations of the cell, and indeterminate as concerns other prolongations.

Discussion of a particular case.—One of the most aberrant and most difficult forms to classify in the empirical law formulated above, is that of the posterior radicular neurons of the spinal cord. The cell of each of them is situated in the spinal ganglion; the axon is morphologically represented by the prolongation which arises from it, and itself divides in the form of the letter **T**, to proceed on the one side to the spinal cord, and on the other, to the cutaneous investment. The dendrites, for a long period ignored, have been discovered by Dogiel: these are the prolongations which arise from the cell, and which terminate in the ganglion itself, in contact with terminal arborizations belonging probably to the great sympathetic.

If such a neuron were obedient physiologically to the law of polarity, understood in its ordinary morphological sense, it should receive impulses only in the ganglion, and should distribute them thence to the spinal cord and to the skin simultaneously.

And it may even be added that, if such a neuron were met with in any other locality less accessible to the isolated stimulation of its branches, there would scarcely be hesitation in attributing to it a conductive capacity in the sense which has just been alluded to. But experiment shows us here that the two branches of the axon conduct the impulse, not merely as the formula would require, away from the cell (in the cellulifugal direction), but the one impulse approaches the cell from the skin to the ganglion (cellulipetal), while the other proceeds from the cell, from the ganglion to the spinal cord (cellulifugal) in such a manner that it traverses the two prolongations placed end to end, just as would be the case with a single fibre proceeding from the skin to the spinal cord.

Concerning the exact connexions of the dendrites and of these remarkable neurons, and the nature of the exact direction of their current of excitation, experiment is silent, because it is impracticable under given conditions with the methods which are available to us. It is thought, however, with some probability, that the principal current is that which, proceeding from the organs of touch situated in the skin, is conveyed in the grey matter of the spinal cord. This physiological argument is looked upon by some as of such importance that it dominates all the others, and they call "*dendrite* every cellulipetal prolongation and *axon* every cellulifugal prolongation" (Van Gehuchten). But then, obviously, these designations lose their morphological meaning in order to acquire one which is purely functional, and which depends exclusively upon experiment.

Relative importance of the different prolongations at different ages.—It has been long known by certain definite indications, such as relative size and precocious development, that spinal ganglia have, at a certain period of intra-uterine life, an important function which progressively diminishes with the development of the nervous system, and which is relatively wanting in the adult. The new anatomical methods require that embryos or young subjects be studied; it is necessary to determine in the adult if there exist intra-ganglionic connexions which can be revealed by the use of these methods.

Adaptation of the Neuron to successive functions.—In assuming that the traces of these structures may be definitely persistent, the example of the posterior radicular neurons shows us how the functional evolution of a nerve element may adapt its several parts to functions altogether different to those which are discharged by the equivalent parts of other similar nerve elements, to such a degree indeed as to invert the direction of the conduction; a new proof, if such were wanting, that structure does not predicate function, and that conclusions must be drawn from the first concerning the second only with the greatest caution. The morphological law would appear to have its own grounds different from those which initiate the physiological or functional law; it is not possible, therefore to substitute the one for the other by confusing them in one common statement.

The Mixed Axon, or the Axon with a double inverse Conduction.—Avoidance.—The progress of the impulse in the nervous prolongations, its concentration in the axon, its dispersion in the collateral and terminal ramifications, its passage through the body of the cell, the manner in which it enters or quits the latter, are so many questions which experiment cannot resolve in a direct manner, and on which only tentative opinions can be expressed. As regards the sensitive radicular neurons, a question of this kind arises concerning the median prolongation of the **T**, which laterally connects them with their cells of origin. According to

Cajal, the impulse transmitted from the skin to the cord avoids this lateral prolongation, and thus saves itself the journey to this cell. According to others this prolongation, more voluminous than its two divisions, would represent the association of their fibrils (Ranvier), which are thus, in the same axis cylinder, some cellulipetal, and others cellulifugal. Thus a *mixed axon* would result, if by this qualification *mixed* is implied elements (here fibrils) which possess the faculty of conduction in opposite directions.

It is impossible to give a decisive opinion for or against these two modes of regarding the question. For those who maintain the possibility of the propagation from one neuron to another by simple contact, there would seem to be no impossibility in the passage of the impulses from one to another group of fibrils in the interior of an axon ; but it must be observed that the special nature of this so-called contact is unknown to us in these two circumstances, and that we are reasoning on resemblances or crude analogies.

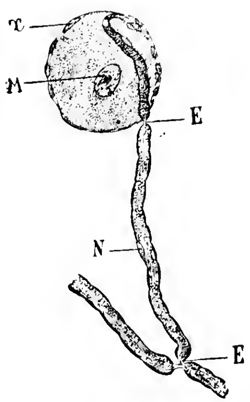


Fig. 11.—Cell of a spinal ganglion in the rabbit.

Its single prolongation is united to a fibre of the posterior root at the level of an annular node, whence its T-shaped appearance ; E, node of the T-shaped tube ; N, nucleus of the first segment of the cellular branch of the T ; E′, first node of the cellular branch ; M, nuclei of its capsule.

However, Bethe, in experimenting on the crab, in which these median prolongations have all the same orientation, has been able to divide them with one cut, and thus to separate the cells of origin from the sensitive fibres which appertain to them ; and he has observed that after this separation cutaneous stimulation still gives rise to reflex movements, although the latter are weakened.

The neuron ramifies at its two extremities ; it receives impulses by numerous and spaced prolongations ; it distributes them by its branches which are generally very widely dispersed. On this subject a problem arises which we cannot resolve, but which must not be ignored.

The impulses which the several dendrites receive converge on the axon ; do they mix in it, as does the blood in the venous trunks which arise from the capillaries ? Or do they follow parallel and independent paths in the axis cylinder ? In other words, do the collaterals, each individually, enter into a determinate connexion with the dendrites ; or are they all connected with each dendrite, and reciprocally ?—The network which is observed in the interior of the cell, and which is found on the passage of the dendrites to the axon appears to furnish the reply to this question. Whether this network is limited to the cell, or whether the reticulated arrangement is continued over the whole extent of the axis cylinder, a formation such as this is able to give to the distribution of the impulses a special character which may be described as neither absolute independence nor complete mixture, but a rearrangement which obeys special laws and which may vary according to the function of the neuron. The specific nature would depend in a certain measure upon the latter.

Objections.—The theory of the neuron, on its first appearance, rapidly gained ground, not only with neurologists, but with the whole scientific world ; and it may be said that it has not, speaking generally, lost favour, either with the former or with the latter. However, if it has preserved its supporters, it has met with determined adversaries, who do not despair of finding it wanting in some essential point. Their most serious objection is that the limitations of the neurons, rendered so obvious by the chromate of silver method (isolated impregnation of

some neurons in the middle of others), may be an artificial result which is due to the action of the re-agent employed; thus has arisen once more the discussion on the *continuity* or the *contiguity* of the articulated prolongations of these neurons.

It does not enter into the object of this work to take part in these technical discussions: the question which has thus arisen, whatever may be its importance, must be fought out by anatomists. But it seems that, in pursuing this detail, the essential point which this large and admirable collection of observations has so vividly brought out, the essential point of view has been lost sight of. This point is the *individuality* of the nerve element, of the neuron. For a long time this was unknown to us. It was generally admitted that the nervous system is formed of two species of elements, fibres and cells, and the point of departure between them was placed in a locality where it is clear that there neither was, or had been at any period of development, any discontinuity. We now know that in the nervous system there is no fibre which is not the prolongation of a nerve cell, and when this fibre passes from one cell to another, we can affirm to which of the two it belongs. Thanks to the new methods introduced by Golgi, the nerve element can now be demonstrated as regards its general structure, its exact boundaries and its principal details.

3. **Individuality of the Neuron.—Its proofs.**—The two following facts established, one by embryology, the other by the method of degeneration, are convincing on this most important point.

(1) *The nervous elements, the neurons, arise from independent cells*; these cells, as His has observed, give out prolongations in different directions, in order to be mutually connected and to associate themselves with the fixed elements of the organism.

(2) When the prolongations are separated from the cell by section *they become the seat of a degeneration which terminates precisely at their extremity.*

In leaving undetermined the question whether these prolongations have contracted connexions which establish their continuity by means of welding, or whether they remain in simple contact, these two facts prove to demonstration that each nerve cell, each neuron, has a definite territory, instead of the indeterminate distribution which the hypothesis of a vague network connecting the cells formerly held to be the case. Further, we can recognize the limits of this territory. Hence it follows that the individuality of the nerve elements is no longer a contestable matter. His has remarked that the nerve elements proceed from cells definitely separated the one from the other, and that these latter give rise to polar prolongations with free extremities, of which one especially is of long extension, in order to form the different connexions of the nervous system.

Ranvier had also seen that the regeneration of nerves, after section, was effected, just as is their origin, by a progressive budding of the axis cylinder towards the localities to be innervated. These facts, however, had not attracted attention, and all the conclusions to which

they point had not been deduced from them. But when, by Golgi's method, it was possible to demonstrate by preparations in which the detail of the prolongation was clearly visible; when, above all, Cajal had given a correct interpretation of them, then only a light was thrown on the subject, and the nerve element appeared in its true limits, very different, it must be admitted, from those which were formerly attributed to it. Whether these elements have their ultimate fibrils simply in *contact*, as many believe; or whether there is between them a continuity by *welding*, as others maintain, is certainly a detail of importance, because in science nothing is a matter of indifference. But, from the special point of view of the individuality of the neuron, it is a secondary question. The limits of the latter are certainly as has been described. Starting from cells separated, and sometimes widely separated from one another, the prolongations which thus proceed to meet each other were in the first instance necessarily discontinuous. Whether they are free or whether they are welded, they do not cease (as degenerations show) to belong each one to a different cell, instead of forming an indefinite network as was formerly supposed.

In studying the nervous system of invertebrates by the aid of the new colour method, St. Apathy and Al. Bethe have discovered in the neurons of these animals a fibrillary network which is present in the cell, and is continued into the prolongations of the latter. To this network they ascribe a fundamental rôle in the production of nervous phenomena strictly so-called, reserving to the cytoplasm of the cell a purely trophic function. As a result of these observations, the theory of the neuron is once again plunged into discussion.

The arguments which have been drawn from these observations are in reality of two kinds, and quite independent: the validity or inaccuracy of the one does not imply the validity or inaccuracy of the others, or reciprocally; hence it is necessary to examine them separately. These arguments are as follows: (1) The neurons being, so far as regards their really nervous portions, formed of fibrils, if it can be proved that these fibrils are continuous from the one to the other, the individuality of the neurons must be compromised, and this the more because, in the opinion of these authors, the connecting fibrils interposed between the cells would appear to effect a sort of independence as regards the latter. In this way a return would be made, under a somewhat new aspect, to the old division of nerve elements into fibres, on the one hand, and cells on the other. As a matter of fact, neither of these two authors claims to have proved this continuity of fibres from one neuron to another; it is a supposition which appears merely probable to them. The arguments given above in favour of the individuality of the neurons remain unimpaired. (2) The fibrillary portion being that which is alone essential to the performance of the strictly nervous functions, and the cytoplasm being reduced to a merely trophic function, the nerve cell would no longer play the preponderant part which has been conferred upon it in nervous acts properly so called, in physical functions for example. This second question is altogether independent of the preceding one; it concerns the internal organization of the neuron, while the first involves the organization of the nervous system by the connexions established between its elements. It is capable of a solution which, whatever it may be, predicates nothing for or against the individuality of the neuron.

Trophic and functional Protoplasm.—In taking into consideration all the data of observation and of experiment which are available concerning the nerve element, I arrived at this conclusion; viz., that two portions, two different protoplasms, must be distinguished; the one, primitive or *organotrophic*, is that which is visible in the nerve cell, in which the nucleus of the latter is immersed; the other, *functional* or *nervous* strictly so called, is that whose properties we are able to observe in the axis cylinder, when we have separated this latter from its cell of origin.[1]

Without any doubt the plane of separation between the two is not marked out by the cut of the scalpel, executed by the experimenter in order to render apparent either the trophic rôle of the one or the functional rôle of the other. This surface of separation seems to be accurately defined in the preparations of Apathy and Bethe.

Having thus localized (in the interior of the neuron) nutrition on the one hand and function on the other, it is necessary to understand that these phenomena are mutually interdependent, and that the structures which represent them are, hence, in a constant condition of exchange and of mutual dependence. In the neuron, in every cell, as in the entire organism, nutrition and function are but very distinct points of view of an assemblage of functions, all of which tend to the same end: the conservation of life.

4. **Physiological data.**—Before the doctrine of neurons had been suggested, physiology had already furnished proofs that certain nervous elements terminate in a definite manner in certain localities which experiment pointed out. These localities correspond exactly to certain of those in which anatomy really establishes the points of contact between the neurons, namely, the ganglia of the great sympathetic. In order of precedence, these are the facts on which this opinion was founded.

(1) If the chain of the great sympathetic be stimulated below the first thoracic ganglion (with reference to the vaso-motor nerves proceeding to the ear), the auricular vessels contract. If this chain be stimulated above this ganglion, these vessels dilate. *The dilators of the auricular vessels end in these ganglia* (Dastre and Morat).

(2) If the sympathetic chain be stimulated either above or below the lumbar ganglia (with reference to the inferior extremity), the hair stands on end in certain areas of the latter. But if these ganglia be impregnated with a solution of nicotine, stimulation applied below continues to cause erection of the hair, but when applied above has no effect. *There is a spino-ganglionic element which possesses the function of erecting the hair and which terminates in the ganglion* (Langley and Anderson).

The specific nature of the Neurons.—In accordance with the law of division of labour, which we find is applicable to the nervous system, as to the whole organism, the neurons should possess specific functions.

[1] This is clearly the idea which has been reproduced under slightly different names, of distinguishing in the neuron a *tropho-plasma* (tropho-protoplasm) and a *kineto-plasma* (functional or nervous protoplasm strictly so-called).

It was at first thought that this specific action was connected with certain external morphological characters of the neurons, that, for example, all those which experiment proves to be sensory would correspond to a definite, externally recognizable, type ; all those which are known as motor, to an equally definite type, but differing from the preceding one, etc. . . . This induction has not been verified. The study of morphological characters, in proportion as it is carried out by the aid of more perfect methods, has rather tended to collect together the neurons discharging all functions under a common type, recognizable among a great variety of forms, but of which not one corresponds to any function with which we are acquainted.

This rebuff is due to the fact that the reasoning on which these observations were based was fundamentally erroneous. The functions, of which up to the present time the connexion with the individual form of nerve elements has been investigated, are not localized in these elements, but in the systematized groups of which they form a part, and whose function they regulate in a certain manner. By itself the neuron is incapable of causing either movement or sensation, far less ideation ; but it originates these several functions in the organs or the complex systems with which it is itself united. In other words, motion, sensation, ideation are not cellular functions, but systematic functions. They are not simple facts, but synthetic expressions implying the co-operation of a large number of elements, whose individual function is not perceptible in the perfected whole. The existence of specific systems, corresponding to specific functions, nevertheless postulates that the order of their elements is different in each of them. There is then, on passing from one system to another, a *specificity of connexion* amongst those elements which causes one to react in a different fashion from the other. Finally, a system, considered apart, is not the indefinite reproduction of the same element, but necessarily consists in an aggregation of parts or of differentiated elements, without which its function would be merely that of this element, magnified indeed or multiplied, but without other alteration. It must be then that the nervous elements present a certain individual specificity, in the aggregations which they form ; but this specificity must be sought for in other ways and on other foundations.

The fact of the name of system being sometimes applied to cell groups which are in reality in no sense systematized, has contributed to bring about this change. The muscular structure, for example, consists merely in the repetition of a great number of elements, whose cellular function is obvious (irritability manifesting itself by the definite contraction of its protoplasm) ; by itself it is not a system, but its elements,

mutually attached and connected with the organs of sense by nervous elements, make up functional systems which are more or less complex, such as that of respiration, of phonation, of speech. In systems thus built up, the initial elements (organs of sense) and terminal elements (muscles), have very obvious cellular functions, while those of the intermediate elements (nervous) elude direct analysis. Hence the cellular function of the muscles has often been transferred to the nervous system (motricity), and hence also the total function of this system (sensation) has been compared to a cellular function of its elements. These inaccuracies in the use of terms must be rectified, otherwise error and confusion will result.

Varied forms.—A large number of neurons appear at the first glance to depart widely from the general type described above ; it is possible, however, to bring them back to it without much difficulty. The body of the cell is not necessarily situated in the vicinity of the receptive pole, but may occur also in the course of the axon, as in the ganglia of the acoustic nerve. Further, certain cells (for example those of the spinal ganglia) are called *unipolar* because they give off but a single prolongation ; but it is known that this single prolongation bifurcates like the transverse branch of a **T**, in order to send a fibre to the skin and another to the spinal cord, both terminating by ramifications, in such a way that the two poles can be found there without difficulty. The reason of this singular arrangement is not known to us, and the function of the median prolongation to which the cell is suspended is equally obscure. It is possible that the impulse avoids it wholly or partially, as Cajal maintains ; it is possible that an inverse double root may exist in this prolongation, which assures its circulation in the cell, as Renaut holds.

In certain neurons the axon, instead of being single, very soon divides into two branches, which sometimes follow different directions for a great distance and sometimes even proceed in opposite directions.

Amacrine Cells.—Certain cells which are entirely embedded in the grey matter, or in the membranes which recall its structure, as the retina, are furnished with numerous arborescent prolongations, amongst which none is detectable which morphologically represents an axis cylinder or axon. It would not be right to maintain from such an arrangement that in these elements the direction of conduction is a matter of indifference : it can only be said that this direction is unknown to us. In none of the localities in which it is available, does physiological experiment, made *in situ*, prove the existence of any instance of indefinite conduction ; but, on the contrary, this latter appears to be everywhere effected in a perfectly definite manner.

Nervous Amœboism.—The mode of termination of the nervous prolongations, whether free or fixed, is connected with a problem different from that of the individuality of the neuron. If the neurons are fixed they are necessarily mechanically immobile ; if they are free from attachment they are capable of receding and approaching one another under certain conditions which are not yet ascertained. Rabl-Ruckard, Lépine, Tanzi, M. Duval have appealed to displacements of this character in order to explain the dissociations, variations and functional paralyses which are observed in health and in certain maladies.

To these supposed movements M. Duval has given the name of *nervous amœboism*, a very definite expression, but one which, by comparing the extremely differentiated prolongations of the nerve cell to the pseudo-podia of an amœba,

clearly goes far beyond his meaning. As a matter of fact, do movements of this kind (analogous to muscular contraction) take place in the nerve terminations?

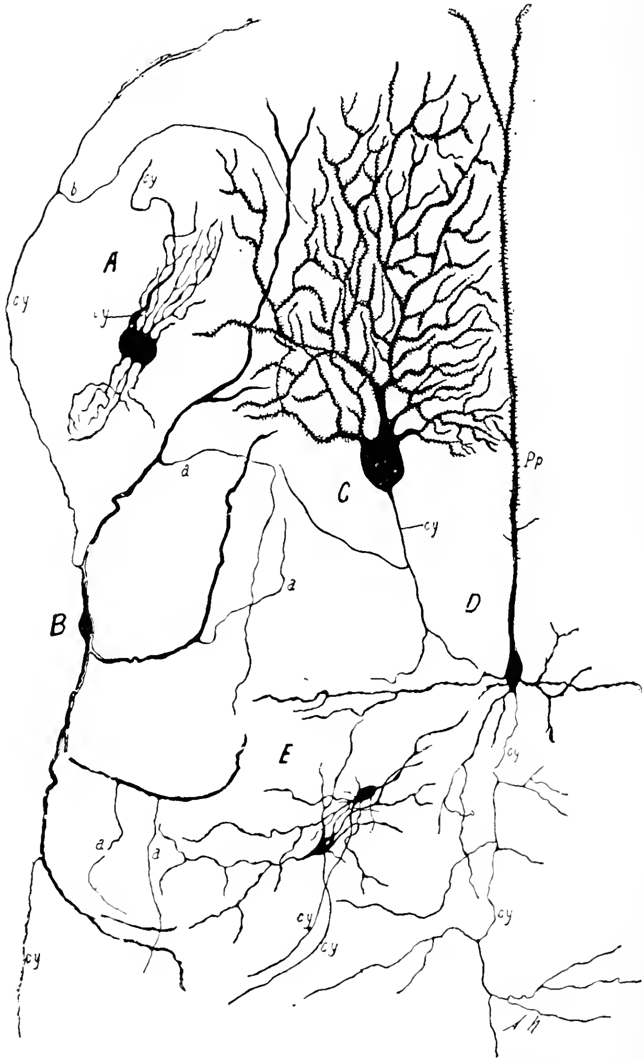


FIG. 12.—Different types of nerve cells coloured by the rapid method of Golgi.

A, nerve cell of the superior cervical ganglion of a human embryo of 25 centimetres (after Van Gehuchten).

B, cell of the molecular layer of the cerebral cortex in a rabbit aged eight days (after Ramon y Cajal): *cy*, polar or principal axis cylinders; *a*, supernumerary axis cylinders starting from different protoplasmic branches; *b*, ramifications of the axis cylinders.

C, cell of Purkinje, from the cerebellar cortex of a cat aged fifteen days (after Ramon y Cajal).

D, large pyramidal cell of the cerebral cortex of a mouse aged one month (after Ramon y Cajal); *Pp*, peripheral spiny protoplasmic prolongation.

E, two root cells of the anterior horns of the spinal cord of a fowl at the eighth day of incubation (after Van Gehuchten).

In all the diagrams, *cy* indicates the axis-cylinder prolongation.

Changes of form in the Dendrites.—Demoor, Stéfanowska and Manouélian claim to have demonstrated that, independently of the slow movements of growth of the prolongations during their development, there are other extemporaneous movements, which give to these prolongations variable appearances and dimensions, following two conditions, the one of activity, and the other of repose. In examining the dendrites of the cells in the brains of animals killed in these two conditions, these authors have found that they differ in the following points.

In the one case these dendrites bear at their extremities and laterally pyriform prolongations; these are met with in brains investigated in their normally active condition; in the other case these prolongations have disappeared into the trunk which supports them, which has assumed a varicose aspect in conse-

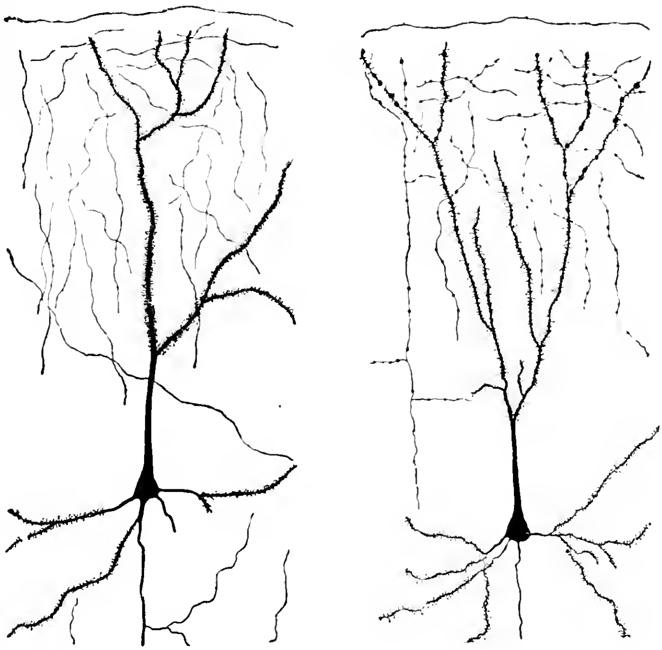


FIG. 13.—Pyramidal cells of the marmot in two different conditions (after Querton). On the left, pyramidal cell of the marmot awake; on the right, that of the marmot asleep.

quence of their absorption: this condition is met with in morphia poisoning, anæsthetic sleep, and sleep succeeding prolonged fatigue, itself the result of violent stimulation.

The preceding authors are unanimous in regarding these changes of form as explaining the two conditions, the one of functional activity, the other of abeyance of function, of nervous groups: the first of these two conditions being rendered possible by the establishment of connexions between the elements which help to make up a system, the second resulting from a temporary rupture of these connexions.—Whether these changes are definitely connected with special states of the nervous system, may be decided by experiment; but that they explain these conditions, is more difficult to admit. Kölliker has brought forward the following arguments against nervous amœboism: the axis cylinder on which we are able to experiment is not contractile; the nervous prolongations

which can be followed into the tissues in transparent animals show no visible movement.

Functional dissociation; Mechanism and localization.—Concerning the existence of a nervous amœboism properly so called, we have just made express reserves which are rendered necessary, we consider, by the want of precise information regarding the functional mechanism of the neuron, and the difficulty of attributing a causal signification to the anatomical and experimental facts by which it has been attempted to explain this mechanism. Having made these reservations, we consider, nevertheless, that the fundamental idea on which this conception is based deserves to be weighed, and that there is something in it which is worthy of discussion. It is this idea which it is now necessary to evolve.

The study of the nervous system displays it to us as presenting during its functional activity, dissociations and associations of its different parts, which are sometimes isolated the one from the other, sometimes united, according to the nature or the complexity of the act to be accomplished. It being admitted as proved that such separations and reconnexions arise in the nervous system, it is natural to suppose that a rupture and a renewal of the connexions between its several parts should be effected, especially in that locality where its elements (nerve cells), in giving off their opposed prolongations, have first encountered each other in the course of their development in order to build up the system in its totality and the sub-systems which compose it.—Thus, in so far as these phenomena of dissociation and association are localized at the extremity of the neurons (at their points of contact), which the study of nervous functions renders apparent, no risk of self-deception arises, whatever may be the modifications or the facts which the future may reveal as necessary to our present conceptions with regard to the constitution of the nerve element. It seems, indeed, that it is here (at the point of junction of the neurons) that the principal transformations which the impulse undergoes in passing through the grey matter take place. Fundamentally, what is generally described as a *centre* is merely *a locality where the neurons are able to organize themselves into a definite system (partial) in order to perform a definite function.*

But to this problem of *localisation* another is added, concerning the intimate *mechanism* of the transformation brought about in the grey matter every time that its organization adapts itself to the performance of a special act. Do the breaks and the union between neurons consist in mechanical and visible displacement, or in molecular movements which our optical appliances do not permit us to recognize? At the present time it is impossible to express a definite opinion on this question. Dissociations and associations between nerve elements certainly exist; in all probability they may be localized in the grey matter at the points of junction of the nerve elements. No definite statement can be made concerning the mechanism by which they are carried out.

Nevertheless, as mechanical phenomena properly so called are those which are most easily comprehended, as they are those which, in the study of every function have always contributed to furnish the first intelligible ideas, the doctrine of amœboism, by clearly defining the question of the connexions between nerve elements, indicates progress in the study of nervous physiology. From another point of view, it has led to the production of works and to the determination of facts which, however obscure their signification may be at the present time, are yet of great interest.

Connexions of the Neurons.—The individuality of the neurons is proved; it is founded on the idea of their exact limitation and of their independent life. It remains to ascertain the mode of connexion which exists between them and the other tissues. On this point it may be said that scarcely anything is known. Whether in the purely static condition, or whether in the dynamic condition, the data we possess concerning these connexions are very incomplete.

The terminal and collateral arborizations of certain neurons come into contact with the initial arborizations or dendrites of other neurons. *The collaterals and terminals of the neuron form no connexion amongst themselves, any more than do the dendrites.* Such is at least the view generally maintained. Nevertheless, Renaut, studying the retina by means of methylene blue, has sometimes observed two cells united by a large protoplasmic expansion; each one has its dendrites, one only gives off an axis cylinder; he calls these *twin neurons.* On other occasions two neighbouring cells, possessing their axis cylinders and protoplasmic prolongations, are united by one of these prolongations; these he calls *coupled neurons.*

FIG. 14.—Termination of neurons in the secretory elements of glands.

A, cell of the parotid gland in the rabbit; B, cell of the mammary gland of a cat during gestation.—The terminations have no connexion with the nuclei of the cells, but only with their differentiated protoplasm.

Adhesive supports.—Even by leaving aside these exceptions to the general law, it is very difficult to gather together the connexions between neurons in a single formula. Contact of the collaterals and terminals occurs, not only as regards the dendrites, but also often with the body of the cell which receives the transmitted impulse. On the other hand, this contact is effected not only by the extremities of these prolongations (axial or protoplasmic cylinders) between themselves, but also for a certain extent of their length. The two orders of prolongations form networks and felting, which render it possible for the same order to enter into contact with several others, or several times with the same. These are the multiplied contacts which Renaut terms *adhesive supports.* Observing, on the other hand, that the protoplasmic prolongations present, under certain conditions, a *beaded aspect* which he regards as connected with the state of activity of the neurons, this author explains, by the appearance and disappearance of this beaded state, the occurrence of these adhesive supports, which enable the transmission of the impulse from one neuron to another to be effected.

It is unnecessary to further criticise these explanations and other similar ones, each of which is based indeed on some special anatomical fact, but which, in its totality and according to the admission of its author, remains hypothetical. Apart from the fact that the impulse is transmitted from one neuron to another in a definite direction, we are almost entirely in a state of ignorance with regard to this matter. We know neither the nature of the transmitted movement, nor the medium in which it is transmitted, nor the conditions of its transmission. We can, it is true, detect after death changes of form corresponding to such or such a condition which we have induced in the animal during its life; but we must remember that the movements of cellular protoplasm are of diverse nature, in connexion with the different functions of the life of the cells; there is no guarantee that the changes thus observed are of a purely functional nature, the modality of the function being itself unknown to us.

Under the influence of the impulses which are communicated to it, the protoplasm of the body of the nerve cell experiences analogous changes of form, of volume, of coloration, or of the situation of its parts, which may be considered as being of a trophic rather than of a functional nature.

Mitral Cells of the Olfactory Lobe.—The cells of the olfactory lobe are disposed in a typical manner, which is of great value as regards the interpretation of the connexions between neurons. Each one of these cells has a special cellulipetal prolongation whose dendritic arborizations are (in the glomerulus) connected

with the terminal arborizations of the axons of the neurons proceeding from the sensorial portion of the nasal mucous membrane. In the opposite direction it gives off a cellulifugal prolongation, which is an axon proceeding in the direction of the brain. Lastly, these cells emit lateral prolongations, arranged at right angles to the preceding; these last are connected, either directly or by associating cells, with the terminal ramifications of the axons of the centrifugal elements which are contained in the olfactory tract, centrifugal elements which are met with again in the optic nerve and other analogous sensory structures.

The excitations of different origin arrive therefore at the neuron, thus built up, by different routes; none of the elements which are in connexion with it

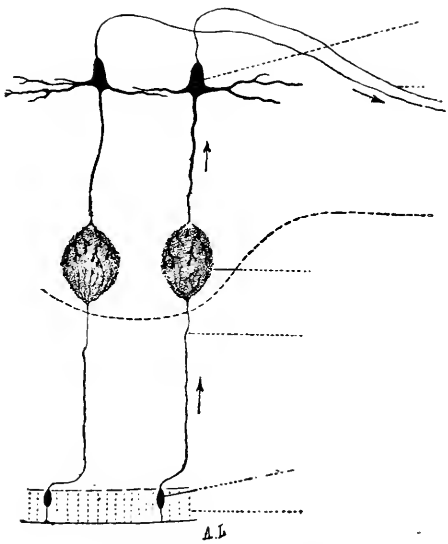


FIG. 15.—Connexions of peripheral neurons with the deep neurons in the olfactory system, at the level of the glomeruli of the olfactory bulb.

The mitral cell receives the impulse in the glomerulus by an elongated prolongation which ramifies in it. The glomerulus is a functional nervous centre.

directly touches its cell. This is a proof that this contact with the cell is in no sense necessary, and that the impulse is received by special apparatus adapted to the purpose.

Pericellular Baskets.—However, there are a considerable number of cases where the connexions between neuron and neuron are effected by the contact of the terminal ramifications of the one with the body of the cell of the other. It is clear that there is here, under these apparent diversities, a general arrangement which enables them to be collected together under a common rule. The body of the cell, more than the nucleus and the other parts which make it what it is, contains the expansion of the fibrils which, in all the other portions of the neuron (dendrites, axon, collaterals and terminals), convey the impulse. When the cell is on the course of the neuron, it is simply passed through by this latter; when it is at its origin, in such a way as to itself form its receptive pole, it necessarily contains the initial extremities of these fibres, which renders them capable of gathering together the impulses, when it is, as often happens, placed on a chief point of bifurcation, or of the ramifications of prolongations, the fibres which pass through it adapt themselves to this distribution, varying

according to the circumstances of the impulse. It is clearly the fibrillary part which, in each one of these cases, assumes the performance of the function which is demanded of it according to its situation.

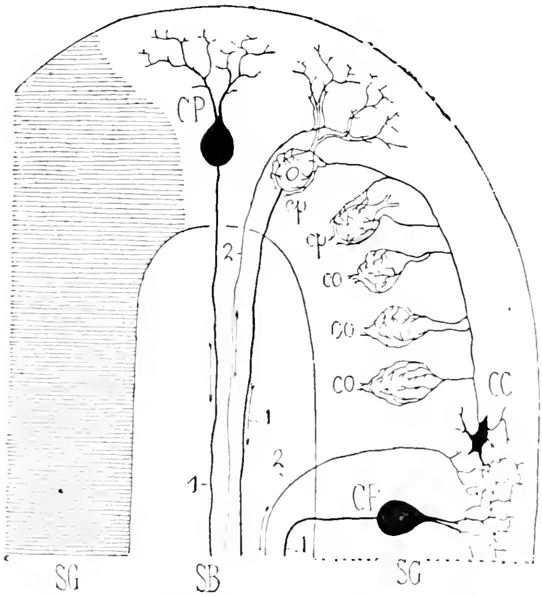


Fig. 16.—Elements of the cortical matter of the cerebellum amongst which is a basket cell (M. Duval).

CC, basket cells; CP, pyramidal cell; *co*, several baskets; *cp*, the basket cell supported by the pyramidal cell.

Spiral fibre: Its signification.—In the batrachia are found, in the ganglia of the great sympathetic, pyriform pedunculated cells on an axon which turns towards the periphery; around this pedicle, as round an axis, is rolled a fibre called spiral, of which the connexions with the cell are noticeable. This fibre is the terminal prolongation of another neuron whose cell is situated higher up, and which has just come in contact, by its ultimate ramifications, with the pyriform cell, through a varicose pericellular network situated between the capsule and the nervous protoplasm (Nicolajew).

B. DYNAMIC CONDITION: FUNCTIONS OF THE NEURON

Each system, individual cell, or organized group, necessarily possesses two orders of functions: the one internal to the system itself, for the conservation of this system (or its development if it is in process of organization and of growth); the other having an influence at the exterior of the system, and which connects it with its surrounding medium, or with a more complex system of which it forms part. Biologically, the first are commonly called *trophic* functions, that is to say, those of *conservation* or *nutrition*; while the second are known as *social*,

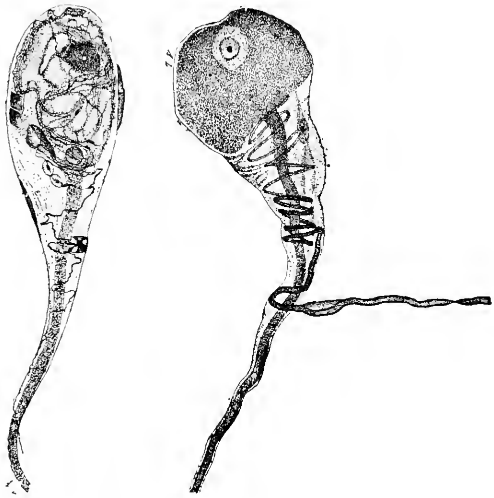


Fig. 17.—Cells furnished with a spiral fibre in the frog.

On the left is seen the origin of the spiral fibre in a fine pericellular network.

that is to say, *those functions which are related to cell elements* of more or less equivalent value.

I. Functions of Internal or Trophic Connexion

The neuron is a living unity; but this unity is made up by the association of complex parts, maintained in a condition of mutual dependence, by which its conservation is assured. These ties between its component parts represent the functions which are internal to the neuron itself, and which, in order to conform to the customary mode of expression, we shall describe as *trophic* or *organo-trophic*.

When, by any means whatever, we break these ties, disorder reigns rampant in this co-ordinated whole; the equilibrium which maintained its form and its existence is destroyed; this form and this existence are both simultaneously compromised; the element, to adopt the usual expression, degenerates. This *degeneration* may entail its total or partial death; in this latter case, when its essential portions escape destruction, reconstruction commences in order to restore the form of the neuron as well as its dimensions and its primitive integrity: this is *regeneration*.

At least three forms of degeneration are distinguished, viz.: *Wallerien* or *descending* degeneration; *ascending* degeneration; *atrophic* degeneration or that resulting from loss of function. All these varieties have this in common, that a local limited lesion, produces alterations which are propagated to a distance in the nerve element or in another element consecutive to it, but each form of degeneration is met with in determinate conditions.

1. Wallerien or Descending Degeneration.—Fontana had already remarked that section of a nerve is followed, after some days, by the loss of its excitability, but to Waller is due the discovery of the laws which regulate the degeneration in its most typical and common form,

descending degeneration, which now bears his name. The following are the conditions of its production.

Experiment.—Let the anterior and posterior roots of a pair of spinal nerves in an animal be cut simultaneously, and after some days examined from the point of view both of their excitability and of their modifications of appearance and of structure ; the peripheral end of the anterior root and the central end of the posterior root will be seen to have assumed a greyish appearance, which contrasts with the normal whitish colour of the two ends. Microscopic examination shows the

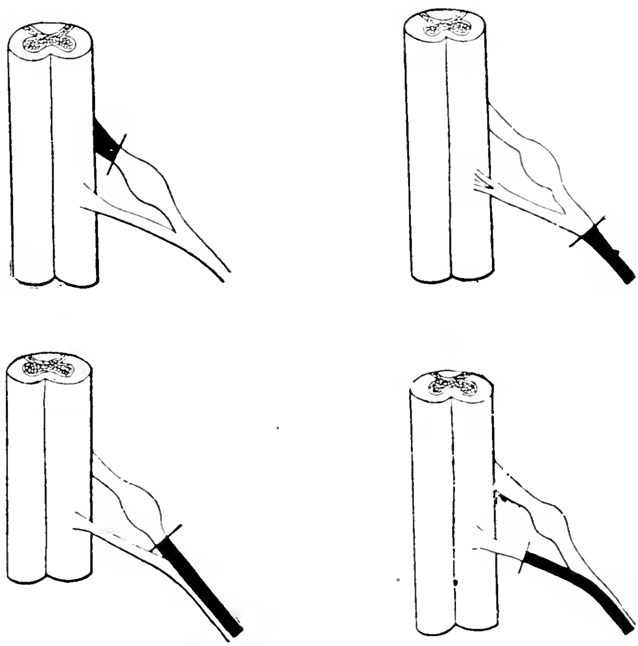


FIG. 18.—Experiments of Waller, on which the laws of degeneration are founded.

Above on the left, section of the posterior root between the ganglion and the spinal cord : below on the right, section of the anterior root ; below on the left, section of the posterior root between the ganglion and the periphery ; above on the right, section of the mixed trunk formed by the union of the roots.

In each case degeneration attacks the segment which is separated from the nucleus of origin of the nerve (spinal ganglion for the posterior root, spinal cord for the anterior root).

presence in this end of the nerve of extreme disorganization. At the same time it is noticed that the two degenerated segments are no longer excitable. Stimulation of the peripheral end of the anterior root, motor in function, as we shall see further on, no longer causes the muscles to contract ; and the central end of the posterior root, sensory in function, no longer excites pain when it is pinched or faradized.

Of the four ends or segments produced by the section, two have not

degenerated : these are, as regards the anterior root, that which remains connected with the grey matter of the spinal cord and, in the posterior root, that which is still connected with the ganglion of this root. Two have degenerated : namely, those which have been separated respectively from one and the other of these two organs. Waller called them their *trophic centres*, and this term is still used.

These two examples appear to show that the degeneration occurs strictly according to the direction in which the nerve conducts the impulses, towards the spinal cord as regards the sensory nerves, towards the muscle in the case of the motor nerves ; as a matter of fact this is not so, as the following experiment proves. If the posterior root be cut, no longer between the ganglion and the spinal cord, but between the ganglion and the periphery, it is the central end which is preserved, and the peripheral end which degenerates. To sum up, *the end which remains intact is invariably that which has preserved its connexions with the cells of origin of the nerve fibres which have been cut*, and the other, in whatever direction conduction may be effected, is doomed to destruction.

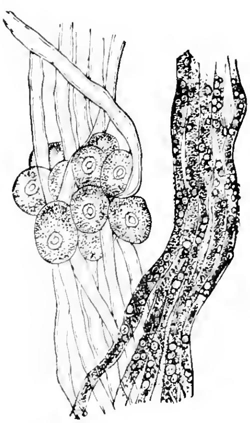


FIG. 19.—Section of the anterior and posterior roots near the spinal cord. Appearance of the fibres after several days.

On the left, posterior root of which the fibres, having preserved their connexions with the cells of the spinal ganglia, have remained healthy ; on the right, anterior root whose fibres, separated from their cells of origin, have degenerated (segmentation of myelin). (Augustus Waller.)

In current language, these facts are interpreted in the following manner : the anterior and the posterior root are formed by the prolongations of the neurons whose cells of origin are, as regards the first, in the spinal cord, and, as concerns the second, in the root ganglion. Every prolongation separated from its cell is destined to be destroyed ; whether axon, dendrite, or the equivalent of any one of these parts its lot will be the same. The cell, on the contrary, which was originally the germ of the neuron, and which possesses the power of preserving it, as it formerly had the power of creating it, is maintained intact, both it and the fibres or segments of fibres which remain in connexion with it.

Remark.—The neurons of the posterior roots, so accessible to analysis in consequence of the arrangement of their prolongations in two directly opposed directions, do none the less form a particular case, which is somewhat rare as regards all the arrangements which the neurons affect. Speaking generally, the body of the cell is found at

the origin of the neuron, in such a way that, from the experimental point of view, a section can only be performed on the axon or the axis cylinder prolongation. Under these circumstances, which are those usually present, degeneration ensues in the direction of the conduction. Hence the method of degeneration may be employed in order to ascertain in what direction impulses are conducted in certain nerve bundles (especially as regards the spinal cord and brain).

Laws of Waller.—1. **Nerves (Nerve Fibres) when separated from their trophic centres (Nerve Cells) degenerate.**

2. The direction of the degeneration is independent of that of nerve conduction

Nutrition and Conduction.—The attempt has often been made to connect the direction of degeneration with that of the conduction of impulses, in such a way as to include the two phenomena in one and the same law expressed by a single formula. The example of the sensory nerves in the posterior roots proves that there is no necessary connexion between them. The process by which the neuron preserves its existence and that by which it conducts the impulse may indeed be related, being mutually dependent, but they are fundamentally and essentially distinct. It is merely necessary to be reminded that, from the morphological standpoint, the case of the posterior roots is a special one. The cellulipetal and cellulifugal prolongations of the spinal cell have therein the same organization, that of axons or fibres covered with myelin; and thus we see that the myelinated fibres are dependent on the cell whatever position they may occupy with regard to the latter. On the other hand, we are not aware of what passes in the protoplasmic prolongations, or dendrites, after they are separated from the nerve cell. It is probable that they degenerate and finally disappear by absorption of their substance.

Trophic and functional centres.—From the distinction thus established between the process of conservation (or of degeneration) and that of nervous function, another arises which is also of importance. Usually "centres" imply localities in which the connexions of similar or different parts are organized and united in order to form a common force. The experiments of Waller prove that the connexions which the different portions of the neuron gather together are centred in the nerve cell, whence the name of *trophic centre* is given to this latter. In their turn the neurons associate and collect themselves together in more or less independent systems, in *functional centres* (or nervous, properly so-called). This association of nerve elements is effected by their prolongations in the complicated connexions contracted by the latter in the interior of the grey matter. Thus the functional centres are distinct from the trophic centres, with which they have been confounded.

Generalization.—The laws of Waller are general laws. They may be verified in all nerves, in the tracts found in the spinal column and in the brain and the great sympathetic system.

Laws of cells.—I consider that *these laws are not only applicable to the elements composing the nervous system, but to every cell element.* Every cell contains an original, germinative, constructive and con-

servative portion as regards form and structure, and a differentiated part as regards its functional relations with other elements. The latter is dependent on the former and cannot exist without it; yet the converse is possible, at all events for a certain time, and in certain conditions.

Loss of excitability.—After section of the nerve, the latter does not immediately lose its characteristic properties. The rupture of equilibrium which results from isolation from its nutritive centre does not exert its full effect until after some days. During this period the nerve preserves a local life, thanks to its vascular connexions. After twenty-four hours it is still excitable; it may be, indeed, that its excitability is increased. *In the dog*, according to Longet, *this excitability completely disappears after four days. In the rabbit*, according to Ranvier, it *disappears after forty-eight hours*; in the pigeon, after two and a half to three days (Waller). In the frog and cold-blooded animals it continues much longer than in mammals. In the first, especially, it varies very greatly according to the season; in other words, according to the temperature. In the frog, in the winter, the excitability may persist up to thirty days after section (Brown-Séquard). Further, this persistence of excitability varies even in the same animal according to its nutritive condition and its vitality.

Structural alterations.—The neuron is a *symbiosis*. The superadded cells form a sort of sheath for its axon (sheath of Schwann), which is separated from the axis-cylinder by an internal layer of myelin. In the cut nerve, the unity between these parts is broken; the myelin becomes segmented; the protoplasm of the cells of the sheath becomes thickened; the axis-cylinder falls in pieces and is re-absorbed; the nuclei increase in number; and the sheath persists as the sole relic of the nerve thus destroyed and deprived of its functions (Ranvier).

In the spinal cord and the brain, in which a genuine sheath of Schwann is wanting, these changes are carried out in a slightly different manner, but the essential result, loss of excitability and disappearance of the axis cylinder, is the same. The neuroglia, by filling up the cavity left by the degenerated fibres, gives a peculiar appearance to a section of the latter which is characteristic of degeneration in a slightly advanced stage.

2. **Ascending degeneration.**—If that part of the neuron which is separated from its cell of origin is doomed to certain destruction, the other portion which has maintained its relation with this cell also experiences the counter effects of this amputation (Nissl). It may be that it degenerates wholly, including the cell; it may be that it survives and, in this case, regeneration of the destroyed portion

may more or less completely ensue; but even when this happens changes in its appearance will be present, indicating internal alterations of its structure.

Conditions which are necessary for survival.—We have seen that degeneration occurs indifferently in the upward or downward prolongation of the cells (as regards the conduction of impulses), whenever these prolongations are separated from them; but in order that it may survive, it is not a matter of indifference to a cellular element, mutilated or not, whether it receives impulses, or is completely deprived of them. If the section is below, it receives impulses although incapable of transmitting them; if the section is above, it is deprived of them, and, in the second case, the cell, having for a time survived its amputated member, finally atrophies and disappears (Van Gehuchten). Thus it is easily understood that section of a posterior root between the spinal cord and the ganglion permits the continued existence of the cells of the latter, while section of the sensory nerve between the ganglion and the skin necessarily causes their destruction (Lugaro). And it can also be understood that section of a motor nerve permits the continued existence of its centre of origin. This persistence is doubtless due to the reflex or voluntary impulses which are transmitted to this centre by the connexions which it has preserved (Marinesco, Goldscheider).

Nature of the change; Chromatolysis.—Whether the cell is to survive or to die, it will present at the commencement the same modifications. These consist essentially in a *dissolution of the chromatic substance* in the enchyleme (*chromatolysis*) which is clearly obvious after a day and a half or two days, but more markedly so after four or five days, and which attains its maximum towards the fifteenth day. This chromatolysis, commencing near the nucleus, extends to the body of the cell in order to attain its prolongations; it is accompanied with a swelling of the cell and with a displacement of the nucleus. If the process stops here, the cell will survive and there will be regeneration. All this disorganization is the result of an effort for the reconstitution of the type of the mutilated element. On the other hand, if matters go further, there will be destruction of the fibrillary network of the cell, disorganization of its protoplasm, and disappearance of the latter (Van Gehuchten).

Its phases.—The alteration which ensues in the cell of the neuron after the separation of its prolongations is only then a true degeneration in certain cases; it is limited in other circumstances (defined above) to a temporary reaction, which is seen to be inevitable, after such an important mutilation of the neuron. Hence the change will present phases whose result differs according to circumstances. The first phase will be that of *reaction;* should the process continue it will lead sometimes to a true degeneration or *destruction* of the nerve cell; on the other hand, it may terminate in a *reparation* of the mischief which has been wrought in the latter. This reparation is manifested by a very marked hypertrophy of the cell, and by its deepened colour due to the abundance of its chromatophile elements; suture of the ends of the cut trunk facilitates this reparation (Marinesco).

Application.—The reaction of Nissl has been made use of, especially by Marinesco, in order to ascertain the nuclei of origin of nerves after total section of

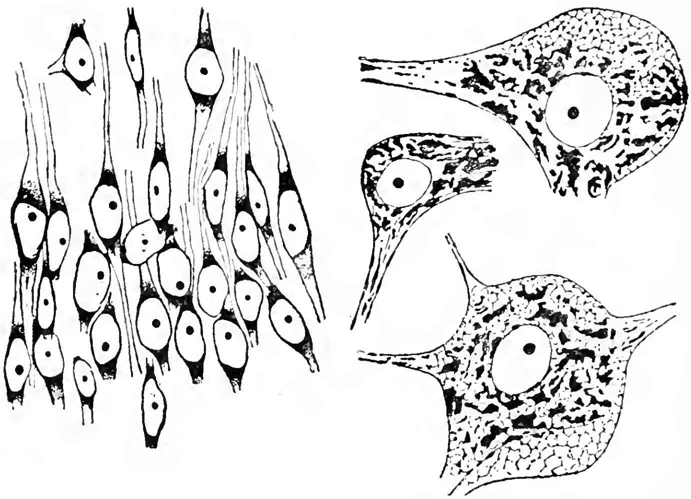


Fig. 20.—Chromophile substance (granulations in black) of several types of nerve cells (after Van Gehuchten).

On the left, bi-polar cells of the cornu ammonis in the rabbit; on the right, three multipolar cells of the nucleus of origin of the oculo-motor nerve. In the degeneration of Nissl the chromatic substance is dissolved from the nucleus towards the prolongations.

these latter, or of merely a part of their bundles of distribution, in order to discover the situation of these nuclei, or rather of the portions of them which individually correspond to these bundles of fibres.

Alteration of the fibres.—Not merely the cells, but the fibres themselves in their journey to them, present modifications consecutively to section, modifications which in the aggregate are very different from those of Wallerien degeneration, which occurs in the fragment cut off from the axon. They are slower than these latter and less deep, and they permit the persistence of the axis cylinder.

This degeneration, known as *retrograde*, which, after section of the nerve, ensues in the extremities of the fibres which adjoin the cell, should be clearly distinguished from the reaction which occurs in this cell contemporaneously with the Wallerien degeneration. The reaction of Nissl and Wallerien degeneration are the *immediate* manifestations of the mischief which ensues in the neuron in consequence of its mutilation, manifestations whose progress is different in the cell and in the cut axon. Retrograde degeneration is a consecutive manifestation, following this mutilation and the disorder which ensues upon it.

All these alterations may be observed in the peripheral nerves and their cells of origin (spinal and medullary), in the elements of the great sympathetic, in the special nerves of the spinal cord and of the brain. Retrograde degeneration is most frequently met with in these latter organs, so that their regeneration is but seldom spoken of, contrary to what is noticed in the peripheral nerves.

Equivocal Sense of the Word.—The words "descending and ascending," used in the sense just pointed out, are ill chosen. In the first place they are faulty, inasmuch as *degeneration does not progress by successively attacking different portions of the length of the nerve, but affects all portions simultaneously, and progresses equally in all portions at once.* Secondly, they are equivocal, inasmuch as they have no connexion with the real position in space of the degenerated segments.

It would be better to speak of *proximal* degeneration as regards the segment which remains in connexion with the cell, and of *distal* degeneration for that which is separated from it.

On the other hand, when it is merely a question of Wallerien degeneration, by far the most easily recognized, in the case of section of the spinal cord, the degeneration will be descending for the fibres whose cells are situated above the section and ascending for those whose cells are below it, without, however, ceasing to be distal.

Ascending neuritis. — The description which has just been given only includes those alterations which follow the interruption of continuity of nerve fibres and the rupture of their nutritive equilibrium, which is the direct consequence thereof as regards the neuron. Under different toxic or pathological influences the nerve may present various alterations, among which the preceding may occur, but which do not concern in a more direct manner the physiological study of the nervous tissue.

3. **Atrophic degeneration.**—Like every cell element, the neuron is susceptible of undergoing, through *prolonged default of functional activity, an atrophy* or diminution of all its component parts without any notable change in its structure. This atrophy is the consequence of the isolation which reaches certain neurons after a time when those which come before, themselves destroyed by degenerative changes, no longer furnish the impulse which is normally supplied to the former. Considered with regard to the union which exists between the elements of the nervous system, section of a bundle of nerves may, in certain conditions, bring about the three orders of degeneration : Wallerien degeneration in the fibres separated from their cells ; ascending degeneration in fibres united to cells ; atrophic degeneration in elements which are deprived of impulses by the degeneration of the preceding.

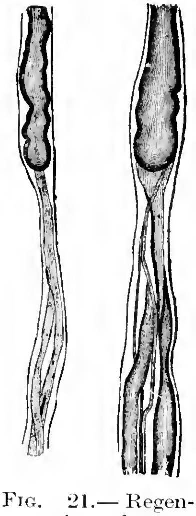


Fig. 21.— Regeneration of nerve fibres, several months after section (after Ranvier).

From the cut extremity of the old nerve fibre one, and often several, new smaller fibres bud out.

Remark.—By these experiments of *merotomy,* we thus are enabled to demonstrate the existence in the neuron of internal functions which establish a dependence between its parts. We are also able, in a certain degree, to localize the functions, by proving that the portions of the neuron which have preserved their relations with the nucleus of the nerve cell are capable of survival, the nucleus being apparently an organ which is essential for nutrition to be maintained. But we know nothing of the reason of this, the intimate detail of these relations being undetermined. And this point is equally unknown to us as concerns every kind of cell as well as the nerve cell.

4. **Regeneration.**—When the nerve cell escapes destruction (which is the rule in ordinary conditions), it undertakes the reconstitution of the segment of the degenerated fibre. The extremity, or the distal end, swells,

sometimes even divides, and in this way supplies one or several growing points, from which axiscylinders take their rise, these latter re-establishing more or less completely the former connexions. When these fibres have again found their way, either within or between the empty sheath of Schwann, regeneration follows its regular course. Vanlair considers that *the rate of growth* is about *a millimetre a day*. The degenerated fibres whose connexions are re-established again assume their functions, and thus their local excitability. Conductivity re-appears before excitability (Duchenne, Erb, Ziemsenn, Weiss).

Nerve suture.—Hence suture of the two ends of a cut nerve favours the speedy regeneration of the cut and degenerated segment. In certain cases the reappearance of the functions of the injured nerve has been so rapid that it has been thought that immediate reunion of the cut fibres has ensued (Schiff, Herzen). It is clear that it is not possible to directly negative the feasibility of such a reunion. But, apart from the fact that it would remain an exceptional case, it is advisable to be suspicious of supplementary phenomena of all sorts which are capable of restoring more or less completely disturbed or vanished nerve functions. The re-establishment of continuity of the nerve should be affirmed only when direct proofs thereof are available : such would be the stimulation of a previously cut nerve, which has been then isolated for a certain portion of its length and stimulated above the suture, and in the case when this stimulation should produce its ordinary effects before the delay necessary for the regeneration of the cut fibres.

Non-regeneration of nervous cells which have been destroyed.— Duval and Laborde, Brown-Séquard, Vitzou have concluded, from their experiments, that regeneration of the nerve centres after partial ablation of certain portions of the same is possible. Juliana, Magini, Schiefferdecker, Cohen, and many others, have protested against these results, and hold with Bizzozero that *the nervous tissue is one whose elements are persistent*, incapable of multiplication and of renewal after destruction. A tendency to regeneration is alone observed ; caryocinesis does not extend to a division of the protoplasm. The tissue which supports the structure, whose power of multiplication is very considerable, attacks the nerve cell and fills up the lacunae left by its destruction (Marinesco).

Suture between centrifugal nerves of different functions.—Calugaréanu and V. Henri, after having divided the hypoglossal and lingual nerves, have sutured the central end of the first with the peripheral end of the second. After the lapse of some months they have noticed an exaggerated function of salivation on the part of the sub-maxillary gland of the corresponding side every time that the animal masticated, as if the motor impulses proceeding from the nucleus of the

hypoglossal, instead of going to the tongue, proceeded to the sub-maxillary gland. Having exposed the hypoglossal nerve above its point of union with the lingual, they have ascertained that its stimulation causes secretion in the corresponding gland of a large quantity of saliva which was capable of transforming starch into sugar.

The lingual nerve contains not only centripetal, but also centrifugal fibres, which come to it from the chorda tympani nerve, and certain of which go to the sub-maxillary gland. The fact discovered by these authors is explained, not by assuming that the fibres of the hypoglossal have become welded with those of the chorda tympani, but that these fibres (at the point of departure of its central end which has been united to the lingual) have swollen out and occupied the empty sheaths of the degenerate chorda tympani, and have come into contact, through their new terminations, with the cells of the sub-maxillary gland which, by their irritation, are excited to functional activity. The motor impulses of the hypoglossal nerve (when the animal eats) become. through this change of route, secretory impulses. The fact is interesting because it proves that *a nerve usually motor in function may become a secretory nerve.* The stimulus which the first communicates to the muscle should be of the same nature as that which the second supplies to the gland, since the one may in a functional sense take the place of the other.

In other words, the process (whose intimate nature is unknown) of the stimulation of organs by their nerves would appear to be the same in every tissue.

Langley has also observed that the central end of the vagus nerve may, when it is united to the peripheral end of the sympathetic, give rise to phenomena of the same nature. Stimulation of the vagus above the reunion of the two nerves produces the ordinary effect of that of the sympathetic.

2. **External connecting functions or nervous functions, properly so called.**—The neuron, when once its personal existence is assured, assumes, like every cell in the organism, a special function in virtue of which it is differentiated. We have already said that *this function* is distinguished from others inasmuch as *it is not, properly speaking, a function initiating energy, but a function which directs energies developed by other cells.*

The methods by which this function is exercised are almost unknown to us, but the aim of the function we are acquainted with. In the nerve something is transmitted in a definite direction ; the nature of this something we are ignorant of ; on the contrary, its objective is clear : it is to cause the organs to pass from a state of repose to one of activity ; in present-day language, to set free their tensions, to expend their potential energies. To this *something* we apply the name *excitation*, an expression which recalls its end, but says nothing as to its modality, and which, for this reason, has no equivalent in physics, where the end of phenomena is not taken into consideration.

The nerve receives impulses at one of its extremities and transmits them at the other.

Internal and external acts, properties and functions.—The external manifestations considered apart, by which the cellular elements of the

organism manifest their *functions*, proceed from internal actions of these elements, which are sometimes called their *properties*. For example: the movement which is amplified by the osseous levers, and which manifests the functional motricity of the muscles, proceeds from an act internal to the muscle, *contraction*, or, if it is thought preferable, from a specific property of the muscular elements, *contractility*. Hence, in order to characterize the dynamic aspect of the muscle, we can refer equally to its property or to its function, because we are well acquainted with both, and the relations of both are perfectly clear.

When we wish to specify the nerve *in actu*, we are much more embarrassed, and the expressions "animal spirits," "nervous influx," "neurility," etc., which have been successively applied in physiological language, without one indicating any superiority over the other, sufficiently prove this. Contractility is the expression of a *definite* change in the form of the muscles, a change towards which all the special acts of muscular tissue converge. Neurility merely expresses the idea of a change *localized in the nerve*, a change which we know must exist, but which it is impossible for us to define.

As we are incapable of defining the internal nervous act, it remains to consider the function of this act, that is to say, its utilization apart from the nerve element itself, in order to give it an appropriate name by which it may be recognized as often as we shall have occasion to speak of it. This function is only known to us from a wholly general point of view, but, in this sense, this knowledge is of extreme importance. It is the *function* which we call *stimulation*.

From a functional point of view, the currents which pass through the nervous system in such a diversified manner are currents of excitation. It is the essential function of the nervous system to be stimulated, and to transmit this stimulus to the organs.

This function, then, is that of each of its component elements which are excited successively or contemporaneously, and which finally give rise to the stimulation of organs which make use of energy under all its forms.

1. **Numerical connexion of the exciting energy with the energy furnished by muscle.**—The notion that the energy given out by the muscular tissue is furnished to this tissue by the nervous system is so widespread that it will be useful to refute it by an experimental fact.

Let the gastrocnemius muscle of a frog, maintaining its connexion with its motor nerve (sciatic), be prepared; and let an artificial stimulus of electrical nature be applied to this nerve; in this way a definite quantity of energy will be expended; as the result of this stimulation

the gastrocnemius muscle executes work which is also definitely known. In this way we can compare the quantity of energy which our exciting apparatus supplies to the nerve with that which our myographic apparatus receives from the muscle.

Energy supplied.—The energy supplied to the nerve by a condenser is less than 0·001 Erg (millieme Erg).

Recuperated energy.—The energy expended by the muscles to raise a weight of 200 grammes 0·5 of a centimetre equals 100 grammes-centimetres, which makes 100,000 Ergs (one hundred thousand Ergs). According to Weiss, who has worked out the elements of this calculation, the ratio of work produced to work expended is

$$\frac{100.000}{0{\cdot}001} = 100{,}000{,}000$$

The recuperated energy is 100,000,000 *times greater than the energy supplied to the small system which is experimented on.*

When it is remembered that the mechanical work of the muscle represents merely a fraction of its total energy, a considerable portion of which is carried off as heat, it will be obvious that the preceding figure is still much below the reality, and hence that the ratio sought for must be still greater.

When, further, it is borne in mind that electric stimulation, however powerful it may be, produces a result which is probably inferior to that due to the stimulation of the nerve by a muscle, or of one nerve by another, it is clear that, as regards the total energies expended by the organism, that of the nerves is quite negligible, without ceasing, however, to be real.

Artificial stimuli, compared amongst themselves, yield also strikingly different results. According to Tigerstedt, when mechanical stimulation is made use of, the ratio of the resulting work to the force of the excitation is about 320; a result which is very weak when compared with that of electrical stimulation.

Conclusion.—The idea (for a long time indeed questioned by physiologists, but still admitted without discussion by physicians) must be abandoned, that the nervous system is a route for the conduction of power in the organism; as a matter of fact it is a pathway followed by an infinitesimal portion of the external energies, which is utilized for the purpose of organizing the employment of force, and which we call *exciting* energy, to distinguish it from the *efficient* energies which we take in with the ingesta, which, circulating in the vessels with the blood, are stored up as reserves in the tissues, and leave the body with the excreta.

2. **Excitability and conductivity.**—By one of its poles the neuron receives stimuli; by the other it transmits them to that which follows it. There is clearly a transport of these impulses in the space between the two poles. These three phenomena, *reception, conduction* and *transmission* or *emission*, which take their origin and play their part in the intimate structure of the nervous element from its dendrites to its intra-muscular terminals in passing through the axis cylinder, obviously suggest to us that they are dependent on the movements of the nervous substance. These movements are invisible; they cannot be detected even with the highest microscopic powers; doubtless they are molecular, but this should not be considered as an invincible obstacle to our acquiring a knowledge of them. In the present state of science our information concerning them is too insufficient for us to form even an imperfect idea on the subject.

Initial shock.—The initial receptive phenomena which communicate the shock to the dendrites of the neuron are unknown to us; the progression of this shock in the axon is also unknown, as is the manner by which it leaves the terminations of the axon in order to reach the element (nervous, muscular, glandular or other) which follows it. We have, however, reason to believe that all these phenomena closely resemble each other, whether taking place in the different neurons compared amongst themselves, or whether in the extremities and the continuity of the same neuron. The infinite variety of nervous actions depends less on the individual variety of the elements composing the nervous system than on that of the connexions and the relationships which exist amongst these elements themselves.

In this connexion, that which passes at the origin and at the termination of the nervous system, taken in its entirety, should not mislead us. It is not luminous waves which pass through the optic nerve, nor sonorous waves through the acoustic nerve, nor a mechanical pressure through the nerves of touch. All of these have been originally transformed by special apparatus (the organs of sense) which have gathered them together under that modality which we regard as uniform, and which, for the sake of convenience, we call the *nerve wave*.

The same reasoning applies to what passes at the other end of the nervous system; the cells, fulfilling such varied functions, which receive this wave must individually possess some sort of apparatus which adapts the uniform impulse, coming from the different nerves, to the special structure and function of each of them. The molecular and unstable equilibrium which the nerves possess the power of destroying in it probably requires to be attacked in a slightly different manner according to the special conditions of each case.

Specific and general excitants.—A *specific excitant* is that which only acts on a certain class of element which is well defined: for example, light in the case of the retina, sound in that of the internal ear.

General excitants are those which act indifferently on every living element and every organized substance.

Every destructive action, such as a prick, traumatism, burn, chemical change, etc., sets up reaction in the substance which it tends to destroy; there is a general cause of excitation with which it is useful to be acquainted, but which is of small value as a method of study.

Electricity in the form of currents, abruptly penetrating the tissues (or even by its distant effects, when the electric perturbation is very strong) is, on the contrary, a very good excitant. This excitant is general, that is to say, adapted to arouse all the cell activities. Further, its destructive action may be rendered practically *nil* when the conditions of its employment are properly chosen.

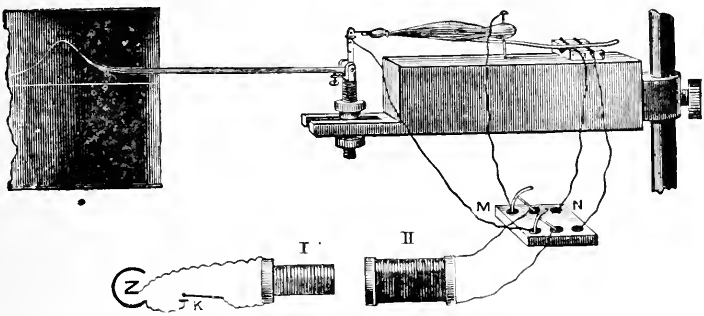


FIG. 22.—Comparative stimulation of a muscle and its nerve, the resulting contraction being recorded on a rotating cylinder.

Z, electric element; K, rheotome or interrupter; I, primary coil; II, secondary coil; MN, commutator carrying the stimulation at will to the muscle by wires connected with its two extremities, and to the nerve by wires connected with a portion of its length (borrowed from Waller).

Electric stimulation has been the means of causing great progress in nervous physiology, because this procedure has rendered the analysis of the different systematic and cellular functions much easier; the little that is known concerning the analysis of the nerve itself is chiefly due to it.

Evidences and estimation of nerve activity.—We say that the nerve is excitable; we notice on the other hand that no alteration is visible in it, no apparent movement; what proof then have we of its activity if the latter consists of purely molecular movements? In order to demonstrate and study this question, there are two methods available, both indirect.

(1) We notice the repercussion of its activity on that of elements

capable of changes of form (the muscles especially) to which it communicates its excited condition. The molecular movement of the nerve arouses a movement, also molecular, in the muscle, which movement is transformed in the latter into a mechanical one, into work, so much the easier to calculate as it is considerably greater than that of the nerve, although being (as is supposed, at least) proportional to it. The *mechanical work of the muscle* demonstrates and measures the molecular work of the nerve.[1]

(2) We render visible and measure, with the galvanometer or the electrometer, the electric motor force which its stated activity produces in the nerve, and which is commonly known as its *negative variation* or its *electric current of activity.*

These two methods have each their advantages and their drawbacks. So long as purely motor nerves are the subject of investigation, the first is without doubt the most convenient and accurate; but when the point of departure of the stimulus is separated from the muscles by a certain number of relays of grey matter, the transformations which these latter produce as regards the impulse which passes through them clearly hinder the muscles from indicating in an accurate manner, as regards extent and succession, the conditions of activity of the stimulated nerve. It is, then, these transformations themselves that the muscles reproduce by their contractions. It is thus only the nerves in direct connexion with the muscles which will be of use in studying the conditions of nervous activity, and the way in which it conducts itself with regard to external shocks. But we, in principle, admit that all neurons, in nearly the same degree, respond in the same manner to stimulation. In applying this principle, the general laws concerning the stimulation of nerves have been deduced more especially from investigations made on those nerves which are directly motor in function.

The second method is applicable to every nerve, to every nerve segment, even when isolated and detached from the animal while it is still living. It requires, indeed, that the nerve be divided at one extremity, in order to receive the derivation of the electric current which is to be estimated.

It is delicate in application, and it is, for want of a better, in many cases by no means a despicable method of analysis.

3. **Isolated Conduction.**—It is allowed, and can be demonstrated, that *the different fibres of the same nervous trunk do not communicate from*

[1] The word *work* is here used in the sense of "expenditure of energy," according to the definition of M. Chauveau, which is accepted by many physiologists.

one to the other any of the impulses which separately pass through them. The only points by which the neurons transmit the impulse are situated at their initial or terminal extremities in the grey matter of the brain, of the spinal cord, or of the ganglia. The necessity of such an isolated conduction, in order that the functions may be properly carried out, is easily understood. If this were not so, nervous functions would be impossible.

A difficulty arises in reconciling this law with that which has just been referred to, of the excitability of the fibres on their course, and of the facility with which the impulses may penetrate them. This difficulty is overcome when it is noticed that this facility is altogether relative. It is sufficiently marked for us to be able, by pressure or electric currents, to arrive at the nerve trunks through the skin, and to arouse them to activity. But it is great enough not to permit mechanical or electrical actions, which are far weaker, and which result from the change of form in the muscles, or of their special current, to act efficiently on them. Further, it must be borne in mind, that these stimuli are artificial, and that we have no right to compare them (as regards efficiency) with the specific excitations of unknown nature (but probably neither mechanical nor electrical) which normally penetrate the nerve and are propagated through it.

Nervous induction.—When two bodies or two systems of similar bodies are in presence of each other and when the play of forces in the one arouses in the other actions similar or analogous to those which exist in the first, it is said that induction occurs. A very clear example of this is furnished to us by the study of electricity, by the so-called *electric induction* and that known as *magnetic.* The word has in these two cases a precise significance, because the conditions of induction are rigorously defined in it. In the study of light, phosphorescence and fluorescence are sometimes assimilated to phenomena of the same order, although the conditions which give rise to them are far less accurately known. When, by stimulation of a sensory nerve, we arouse the activity of one or several nerves (motor or other) which follow it, we may, for our part, see in this re-echo one after another of the same phenomenon through separate elements, an example of induction, but it must be distinctly understood that the word "induction" has here (as all those expressions taken from physics—conduction, reflection, polarization, interference, etc.) merely a comparative value, and in no sense an explanatory one. There may therefore be a nervous induction, as there is a nervous conduction, without the electrical nature of the phenomenon in the two cases being in any way implied. Or, to speak more accurately, we may prove that in the nerve a certain electric conductivity and certain electric or magnetic phenomena of induction exist, without prejudging the real nature of the mechanism of the stimulation of one nerve by another. We are, so to say, assured in advance that the conditions of the physiological phenomenon are not reducible to one of those elementary phenomena of energy which physics demonstrates in a state of isolation in its schematic experiments.

So far as concerns magnetic induction, it must be here once again remarked that special precautions have been taken in order that it may not be produced

by the action of one nerve fibre on another throughout the length of the axons of varying function, which are placed parallel to one another in the same nerve trunk. The activity of one nerve fibre never involves that of its neighbour. It only involves it so far as it is placed in relation with it, in the interior of the nuclei of the grey matter, or of the ganglia. It is this fact, clearly demonstrated, which is expressed by the law of isolated conduction. Throughout the course of the fibres, not only is conduction (electrical or not) isolated, but induction (electrical or not) does not exist. And it was necessary that this should be so in order that the nervous system might discharge its functions of direction, of rearrangement of the impulse which are both variable and complicated, through the tissues of the organism.

The nerve fibre, the axon, is a closed system analogous to that of our telephones. If a point exists by which this system may lose its definite lines of force, so that these may act on lines of force of similar systems, it can only be at its extremities, at its receptive and emissive poles. The structure, still imperfectly known, of these delicate parts shows us nothing which can support the idea of the occurrence of a phenomenon of this kind. The experiments which would be adapted to demonstrate this phenomenon are absolutely impossible of performance. The properties of the bodies and of their surroundings, the nature, the origin and transformation of energy, are in the special case wholly unknown to us. The nerves transmit an impulse with the greatest facility in directions with which we are acquainted ; we are wholly ignorant of the manner in which they transmit it.

4. **Propagation in the two directions.**—In the normal performance of its functions, the neuron receives the impulse exclusively by one of its poles, which is invariably the same ; hence it follows that it transmits the impulse invariably in the same direction, that is to say, for example, from the spinal cord to the muscles in the case of the motor nerves ; from the skin to the spinal cord in that of the sensory nerves. When we stimulate the nerve artificially in its normal position, we have just seen that, starting from the stimulated point, the impulse proceeds towards its habitual destination. But is it possible that at the same time from thence it may be transmitted in the opposite direction, that is to say, contrary to its normal course ? The question has no great practical interest, since it involves abnormal conditions ; but it has an importance as concerns the general properties of nerve substance.

In order to settle the question, it would be necessary to turn the neuron round by inverting its two poles, the receptive end becoming the distributive end, the distributive the receptive, and then to see if the impulses (normal or artificial) are still transmitted in this new position. This total inversion being impossible, it would be necessary, after having removed a segment of the nerve trunk between two sections, that we bring this inversion about, by welding together the two ends and then observing what happens in this new position.

This experiment has been attempted by several authors, especially

by P. Bert, who employed different methods, chiefly on rats' tails, and in his hands it appears to have settled the question. Yet, on considering it more closely, it seems that the objection may be urged that the segment, in this way cut and reversed (even when the operation has been performed at several sittings), degenerates and is replaced functionally by new fibres having the same orientation as the old ones, which obviously deprives the experiment of demonstrative value. The laws of degeneration being known, it would seem that the attempt to give to nerves connexions other than those which they acquire by their development must be given up. Yet a means exists by which we are able to observe the state of activity of a nerve in the extremity in which we believe that the impulse may be propagated. This method is that of the negative variation of the electric currents of nerves.

If it were possible to deal with a nerve trunk either exclusively sensory or exclusively motor (not containing these fibres mixed together in any proportion), this method would settle the question. Unfortunately such nerves do not exist, at all events in the absolute manner required, so that the question must still remain undecided. Without doubt, the nervous system contains an arrangement by which the passage of impulses in a definite direction is assured, just as does the circulatory system. Observation proves this, the evidence being the same in the two systems. In the second case the controlling apparatus is known to us : it is the arrangement of valves by which the cavities of the heart are separated the one from the other. In the first case neither analysis nor our intelligence has been able to unravel the problem. But it may be that there is some remote analogy with the arrangement which holds in the vascular system ; it would be, according to this hypothesis, localized in the points of union of the neurons. Between these points the impulse would be able to travel in either direction, but these points once passed, it would be impossible for it to retrogress.

5. **Integrity of structure.**—If a nerve is cut in its course, it ceases to transmit the impulses beyond the point of section. Indeed, if its two ends are adjusted as exactly as possible, conduction is not effected. It depends on a special structure which has been destroyed in the axon at a certain point of its course. Nerve conduction is indeed a molecular process ; it is rendered impossible by a local derangement, even a very limited one, or an alteration in the arrangement in the molecules of the nerve structure.

Welding of nerves.—Schiff and Herzen have maintained, and surgeons also, that the two ends of a freshly cut nerve, pared and sutured, can unite by first intention, degeneration being hindered, and in this way

the loss of function may be prevented. On the other hand, Ranvier, Vanlair, and with them the majority of physiologists, consider that degeneration is an inevitable consequence of section.

6. **Local excitability of the different portions of the neuron.**—In the normal condition the nerve transmits impulses from one of its poles to the other. Artificially, it can receive others in its course, which comport themselves like the preceding.

If it is cut across its length, the segment attached to its emissive or distributing pole ceases to receive the current from the receptive pole, and consequently to distribute it to the elements, nervous or otherwise, in which it terminates. This isolated segment nevertheless preserves its excitability until it degenerates, that is to say, during two, three, four days or longer, according to the animal.

This temporary conservation of excitability in the axon separated from its cell has an important signification. The axon (like all the other prolongations) depends on the cell for its nutrition, for the conservation of its internal organization. It does not depend upon it immediately for that which we know as its function. Isolated from it, it yet comports itself as an entire neuron. It is capable of receiving impulses and of transmitting them to its extremity. This is precisely the rôle of the nervous system in the organism, namely : to transmit an impulse from one point to another. *The body of the cell of the neuron is an organ necessary for the organization and conservation of the latter, but it takes no necessary and direct part in its power of functional activity properly so called.*

This is a consequence of the general excitability of living matter, but the reactional manifestation is here remarkably clear. Along the whole length of the axon impulses may be made to penetrate the latter : contact, light pressure, extremely weak electric currents equally suffice to render its ordinary action manifest. Hence between the receptive pole and the rest of the neuron there is no essential difference of properties.

Excitability and conductivity.—*Excitability* is the property which the nerve possesses of reacting to the stimulus which it receives, not only from its receptive pole, but throughout its course. *Conductivity* is the property of transmitting throughout its length away to its terminal extremity the condition of excitation which it has received. An attempt has been made to ascertain experimentally if there is not here fundamentally one and the same property, the conduction resulting from parts of the nerve being successively excited the one by the other ; as if the energy liberated at each point acted on the following point by causing the latter to give off its intrinsic energy, and so on. These experiments aimed at subjecting the nerve to different influences, in order to see if the two phenomena present parallel or divergent or even contrary variations.

It may be said that, as a general rule, the influences which modify local excitability modify little or not at all the transmission of the impulse through the part of the nerve thus influenced. Example : a small portion of a nerve being submitted to the action of CO^2, comparative stimulations are applied to the part affected and above the latter (with regard to the direction of the transmission) ; the local excitability is much diminished, while the stimuli applied above are as powerful as ever (Grunhagen). It is the same as regards variations of temperature, local or general (G. Weiss). When a nerve degenerates (after crushing) the voluntary impulses again become efficient, while the nerve is still locally incapable of stimulation by electricity (Erb).

In the reasoning which is at the foundation of these comparisons it is assumed that, as regards the hypothesis of conductivity and excitability being one and the same thing, the artificial excitant (electricity) and the natural excitant (physiological stimulation of one segment by another) possess the same efficacy. Yet, on the other hand, there are reasons for believing that the artificial excitant is less active, and that, if the excitability diminishes, the final advantage must remain with the natural excitant. The strongest argument in favour of the dissociation of the two properties lies in the fact that the temperature does not modify the conduction, and that the latter remains equal to itself in the whole course of the nerve; it is only in these two points that there is still a variance between experimenters.

7. **Rate of conduction.**—The impulses which reach a nerve, at its origin, or in one of its points, traverse this nerve at a definite rate, which it has been possible to reckon. Helmholtz, who was the first to measure this rate in the nerves of the frog, has found it to be about 27 metres a second. Chauveau, who has studied it on warm-blooded animals, has found it to vary according to the nerves operated on, and according also to certain circumstances peculiar to the subject or to the nerve itself. In the horse it is about 70 metres in the motor nerves of the larynx, and only about 8 metres in the motor nerves of the œsophagus.

Method.—The rate (when it is uniform) is the distance traversed in a unit of time:

$$V = \frac{e}{t}$$

In the application of this formula, e represents the length of the nerve from the point stimulated to the muscle; it is calculated without difficulty in fractions of a metre, by direct measurement. t is the time which elapses between the stimulation of the nerve at a given point and the contraction of the muscle; its determination is more difficult and requires special arrangements. The method most generally employed consists in inscribing, on a surface moving uniformly (a rotating cylinder) and at a given rate, the stimulation and the muscular movement on two parallel lines by the aid of styles which are exactly superposed, the one moved by the exciting electric current (electric signal), the other by the muscle which contracts. The time which elapses between the two records is measured by the distance which separates them in the direction of the movement of the surface. This calculation is rendered very easy if, on a third line parallel to the two others, the movements of a tuning fork giving 100 or 200 oscillations a second are recorded.

Length of propagation and latent period.—The calculation thus made may still be incorrect, because experiment has shown that, in its passage from nerve to muscle, and independently of its transmission through the nerve, the impulse undergoes a retardation (or latent period), which it is necessary to deduct from the length of time inscribed on the registering cylinder. In order to overcome this difficulty two successive determinations of excitation are made on the nerve, by choosing two points of the latter sufficiently wide apart. If t be the duration of the transmission of the impulse from the farthest part of the muscle, and t^1 the duration for the nearest point; $t - t^1$ is the time occupied by the impulse in traversing the distance from the first of the points to the second; as to the space traversed, it is the distance which separates the two points, and which is measured directly on the prepared and exposed nerve.

In the first experiments of Helmholtz the values of t and of t^1 were determined by making use of the method of Pouillet.

Let a galvanometer be intercalated in a conducting circuit. If in this circuit a current of a given duration (fairly short) be made to pass, the deviation of the needle is proportional to the duration of the passage of the current. The experiment is arranged in such a way that the current which should pass through the galvanometer is made (that is to say, commences) at the exact moment of the stimulation of the nerve, and is broken (that is to say, ceases to pass) at the exact moment of contraction of the muscle. In other words, matters are so arranged that the stimulation makes this current, and the contraction which ensues breaks the contact which permits it to pass. Two observations are made, by exciting the nerve at two points unequally distant from the muscle. In this way the two unequal values t and t^1 are obtained, whose difference represents the time sought, T.

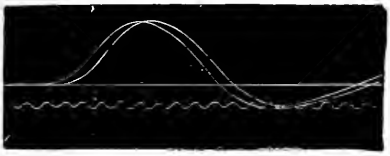


FIG. 23.—Estimation of the rate of conduction in a nerve.

Two contractions obtained by stimulating two points of the nerve separated by a definite interval. The stimulation is made automatically by the rotating cylinder at the same phase of its rotation. The delay of one of the contractions measures the time required by the impulse to pass over the space between the two points of the nerve successively. The duration of this delay is determined by a length which may be estimated by comparing it with other lengths representing hundredths of a second (waved line traced by the vibrations of a tuning fork).

Chauveau, experimenting on the nerves of the larynx of large mammals, which have, as is well known, great length (on account of their recurrent course), has combined graphic inscription of the muscular contraction with the indications furnished by the signal of Marcel Depretz put in action directly by the muscle, while another signal marked the moment of the excitation, and the vibrating style of a chronograph recorded the $\frac{1}{250}$ of a second.

Further, this author, instead of two observations, made three, by stimulating the nerve in three different points. The comparison of the times with the space traversed leads him to conclude that the rate of propagation of the impulse is not uniform, but continually changes during its transmission through the nerve.

C. STIMULATION OF NERVES

Stimulation is a communication of an external movement to our own tissues. It must be added that this communication belongs to the order of *shocks* or of *rupture of equilibrium* ; the movement, once induced, continuing by the expenditure of a pre-existing potential. In this phenomenon, which is known as excitation, there is then a movement-cause (coming from the exterior) and a movement-effect (internal to the stimulated tissue). Usually this last greatly exceeds the first in magnitude ; this being so because it is divided into two effects, of which one is strictly the work of rupture or of shock (equalling the exciting work) ; while the other, secondarily evolved, is a measure of the liberated potential energy.

Gradation of the effects.—In order that the effects of the stimulation may have free play, the exciting cause must attain a certain intensity, below which it is either inefficacious or insufficient. This degree of

energy corresponds to what is known as the *minimum* excitation, or *the threshold of excitation.* If, starting from this degree of intensity, the force of the stimulation varies, two things may happen. In certain cases, as in the muscle of the heart, the effect is not increased. In many other cases there is a certain relationship between the intensity of the stimulation, or that of the shock, and that of the effect produced. The response of the stimulated tissue progressively increases, and attains a maximum which cannot be exceeded : this is the *maximum* excitation. At the precise moment at which it attains this maximum the excitation is *optimum.*

If the excitant still increases in intensity a contrary phenomenon, diminution, results : there is a decrease of the effect produced, which may proceed to its complete annihilation : this is the excitation known as *pessimum.*

All tissues are excitable ; certain of them, like the nerve tissue, are so to a high degree, and are organized in such a way as to be capable of transmitting and communicating their stimulation to other tissues. A muscle supplied with its nerve (in practice a frog's foot whose nerve trunk has been isolated : galvanoscopic foot) is the most convenient subject for the study of stimulation and of its laws.

Various stimuli.—Stimuli may be of very different nature. Some are *natural :* light for the retina, sound for the internal ear, the energy whose nature is unknown by which the motor nerve acts on the muscle . . . are of this order ; each of these, in the circumstances peculiar to itself, reacts on an apparatus which, in the course of phylogenetic and ontogenetic development, becomes adapted to this stimulus rather than to any other. Others are *artificial :* mechanical shocks, electricity, chemical agents . . . by attacking each one of the preceding organs they will elicit its special reaction, although, in the exercise of the functions of any one of the organs, these agents take no part whatever. The same facts may be expressed in other words if we say that, of these excitants, the first are *specific,* that is to say, display an adaptation of evolution, while the second are *general,* that is to say, manifest a common property, or a property common to all protoplasm, that, namely, of reacting to external stimulation.

Electrical stimulation.—Amongst the artificial excitants, electricity is that which is most convenient for the general study of the laws of excitation. Pressure or mechanical shock, even when very slight, may stimulate the motor or sensory nerves, and this means was much employed when experiments for the determination of nervous functions were first undertaken. Certain weak chemical substances, such as glycerine, chloride of sodium . . . may also act as stimulants ; but the rapidly destructive effects of these stimuli and the difficulties which attend their graduated employment much limit their use.

PRELIMINARY IDEAS

It becomes more and more necessary for the physiologist and for the physician to be acquainted with the language of electrology and to be familiar with the exact signification of the ordinary terms made use of in this science, which is more and more appealed to as a means for the study of living beings.

A. Electrical Energy—Its Units

Potential energy.—Metaphorically speaking, potential energy may be defined as a *difference of level.* Two mill courses, two lakes, of which the upper levels are at a different height above the level of the sea, present a difference of potential; if they are united by a conducting pipe at their inferior level, a motor force of running water comes into action, being so much the stronger as the difference of level is greater. Two metallic isolated spheres, equal in size, unequally charged with electricity and united by a conductor, will, in the same way, give rise, in this conductor, to an electric current.

Electro-motive force.—Electro-motive force thus originates in a difference of electrical potential between two given points on the conductor. The absolute value of this potential is not taken into account, any more than the absolute level of the jars in communication, but only the difference between two given values. In the case of reservoirs full of water, the zero potential would be the sea: for the water of lakes and of reservoirs of all kinds runs away into it until it is exhausted, if they are furnished with deep conducting pipes and if the water is not renewed. As regards bodies charged with electricity, the zero potential is the earth: every body electrically connected to the earth loses its potential if its charge is not renewed.

Its unit: the volt.—The difference of potential between two points of a channel of water is measured in metres or fractions of a metre (reckoned vertically); the difference of potential between two points of an electric conductor is estimated in volts. The *volt* is the unit of electromotive force; it is equal to the difference of potential existing between the two poles of a Daniell's element.

Unit of resistance: the ohm.—A force which is conveyed in canals, from the mere fact of its canalization, experiences a resistance which transforms it partially into heat, and which economizes its expenditure to a greater or less extent.

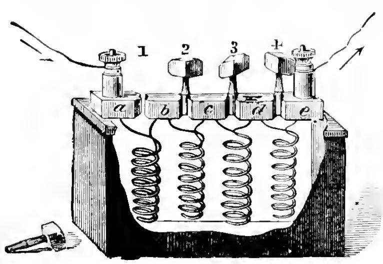


Fig. 24.—Resistance coil or rheostat.
The resistance increases in proportion as the keys 1, 2, 3, 4 are removed.

For a given conductor (electric or not), the resistance will be so much the stronger as its length is greater and its section narrower. The unit of electric resistance is the *ohm*; practically it is equal to that of a wire of annealed copper 50 metres long by 1 millimetre in diameter.

The converse of the resistance is known as the *conductivity*; it is so much the greater as the conductor is shorter and its section is larger.

Unit of Intensity: The Ampère.—The intensity of a current of water is its yield (the quantity which flows in a unit of time); this yield is proportional to the difference of potential (difference of pressure, motive force): it is inversely proportional to the resistance, or directly proportional to what may be called the conductivity of the conduit. If there were no other available means of more easily measuring it, it could be expressed by a relation between these quantities.

Law of Ohm.—The electric yield, or intensity of the current, is necessarily expressed by this same relation.

Let I be the intensity, E the electromotive force and R the resistance; then this equation arises:

$$I = \frac{E}{R}$$

If E is made equal to 1, that is to say an electromotive force about equal to a

Daniell's cell, and R=1, that is to say a resistance equal to 1 ohm, the unit of intensity is determined, that is to say *the ampère*

$$I = \frac{1 \text{ volt}}{1 \text{ ohm}} = 1 \text{ ampère}.$$

Quantity of electricity : coulomb.—In defining the intensity through the ratio of the electromotive force to the resistance, the time is left undetermined. If the time is multiplied by the intensity, we arrive at the *quantity* : $Q = I \times t$, and if we assume that the second is an unit of time, the quantity will be the amount of electricity spent when an ampère is yielded in one second : this is the *coulomb* or *ampère-second*. In commerce the *ampère-hour* has been adopted.

B. Different Electric Currents—Discharges—Currents properly so called

Let there be two surfaces of a different potential : when they are united by a conductor they give rise to a flux of electricity which is known as a *current*. This current may assume different forms and be of extremely different durations.

Instantaneous currents : discharges.—If the surfaces carry charges which are opposed or unequal and which equalize themselves by traversing a simple rectilinear conductor, the flux assumes an extremely rapid form, is, indeed, practically instantaneous ; this is the case with the *discharges* of static electricity. These currents may be usefully employed for the stimulation of nerves in conditions which are correctly known, when condensers of a known capacity are made use of, to which charges of a known intensity are communicated, and which may be directed through the nerve either at their entrance into the condenser or at their exit from the latter, in either direction.

Continuous currents.—If the surfaces are in contact with the source of energy (chemical, thermic, etc.) which renews the difference of potential as the latter becomes weaker, the flow is then continuous, as in batteries and accumulators. The renewal of the potential in proportion to its decline may also be effected by mechanical energy, as in Gramme's machine.

Constant current.—A current is called constant when its value remains nearly the same during its passage.

Polarization.—In certain batteries, of the type of that of Volta, for example, there arises, from the mere passage of the current in the interior of the battery, a contrary electromotive force which is due to the formation of opposing poles by the chemical reactions and the transport of the ions. The hydrogen, set at liberty by the action of the sulphuric acid on the zinc, is borne to the positive electrode, whose apparent conductivity it diminishes ; and, further, this hydrogen in proportion as it increases in quantity, tends more and more to reduce the zinc from the sulphate of zinc formed, whence arises the development of an opposed current contrary to the first, not so strong as the latter, but whose intensity continues to augment through the functional activity of the cell.

Non-polarizable cells.—This inconvenience has been overcome by means of certain contrivances which afford, in principle, to the products formed during the reaction, an immediate point of accumulation by which they are hindered from being deposited on the material which is being destroyed, so that in this way polarization is suppressed by arresting the action contrary to that which gives rise to the current. Thus, in Daniell's cell, the hydrogen formed by the action of sulphuric acid on the zinc is taken up to form water (instead of reducing zinc from the sulphate of zinc which has been formed).

Accumulators.—An accumulator is an apparatus constructed for the purpose of utilizing only the current of polarization, or secondary inverse current, which arises in cells after the passage of their special current, as also in the voltameter

after the passage of an external current. Thus it has been endeavoured by this apparatus (contrary to what is aimed at in cells) to make the polarizing modification as marked as possible. Accumulators are *charged* by causing them to be traversed by an external current for a certain time in one direction. When polarization is once produced, an inverse current of *discharge* is received from it, which is remarkably constant, and which yields up, whether in quantity or in energy, the greater part of the electricity which it has accumulated.

Like the condenser, the accumulator is a reservoir of energy. In the first this energy is electric, in the second it is chemical. In the first it undergoes no essential transformation ; in the second this energy passes, during the charge, from the electric to the chemical state, and conversely during the discharge.

Oscillatory current.—The current, without ceasing to be continuous, may present periodic augmentations and diminutions of its intensity ; it is then said to be *oscillatory.*

Alternating current.—In the electro-magnetic machines of the class of Pixii and of Clarke (rotation of a magnet before a current, or reciprocally), the current obtained presents not only periods of augmentation and of diminution, but is completely reversed at each half turn, unless by special contrivance this is corrected. In both cases it is oscillatory, but when it is not corrected it is *alternating.*

Sinusoidal current.—If, further, the succession of values of the current follows the law which regulates the oscillation of a pendulum, the current is called *sinusoidal.*

Diphasic, continuous and triphasic current.—In the electro-magnetic machines of former days the current, which is reversed at each half rotation, presents two phases at each complete rotation : it is diphasic. In Gramme's machine a special arrangement as regards the rolling of the wire on the electro-magnet permits the production of a continuous current. Other combinations of rolling allow the production of triphasic currents.

C. Induction

Between two electrified bodies attractions and repulsions arise which, when they are satisfied, lead to displacements of these bodies.

Lines of force : field of force. — These displacements follow certain lines between these bodies, which for this reason are called *lines of force.* The space traversed by the lines is known as the *field of force.* These lines indicate, by their number in a given space, the value of the field in this space. The field of force is said to be so much the larger as the lines in it are more closely compacted and more numerous in a given space. They furrow the spaces comprised between electrified conductors, and consequently pass through the isolating bodies, which, for this reason, are known as *dielectric.*

Electric induction.—When a conductor (for example, a metallic sphere) which is isolated is charged positively or negatively, it induces, by its lines of force, in a neighbouring conductor a quantity of electricity of opposite nature, which is exactly equal to its own : this is *static induction,* or electric induction properly so called, by the *lines of electric force.*

Magnetic induction.—When a circuit conductor is traversed by a current, new lines of force are developed in the space which surrounds it, each of these forms a closed circuit and each is perpendicular to the lines of electric force or lines of flow of the current, and consequently perpendicular to the direction of the conductor which it envelops like a ring, and creates in the interior of the circuit and around it a *field of magnetic force.*

If, in this field, another closed circuit conductor is arranged, so that the intensity of the current commences to differ in the primary circuit, the number

of the lines of force varies in the magnetic field ; this variation (positive or negative), at the moment of its production, induces a current (inverse in the first case, direct in the second) in the secondary circuit.

In the conditions which have just been described, *it is the variable condition of the primary current which gives rise to induction in the neighbouring circuit :* during the permanent condition equilibrium once more prevails. Induction may be produced, but in a different fashion, by increasing or diminishing the distance which separates the circuits. In the one case, as in the other, induction ensues when the lines of magnetic force of the primary current change their number in the secondary current.

The number of lines of force which, from the primary circuit, enter into the secondary circuit is so much the greater : (1) as the distance of the two circuits is shorter (these lines individually complete around the conducting wire, diverge more and more as they are removed from the plane in which the circuit is contained); (2) as the planes in which the two circuits are contained are more

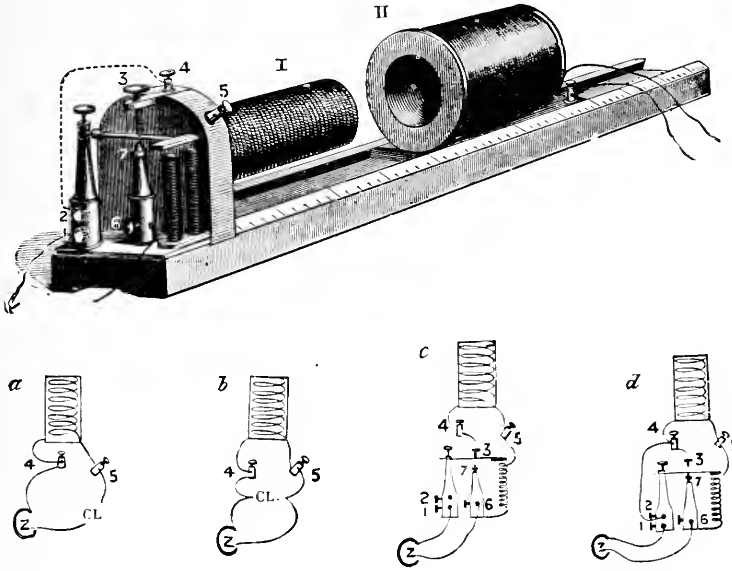


FIG. 25.—Induction apparatus of du Bois-Reymond (after Waller).

I, primary coil ; II, secondary coil, which may be approximated to or withdrawn from the former in order to vary the intensity of the induced current.

a, situation of the key or interrupter CL for producing isolated discharges ; *b*, situation of key in short circuit ; *c*, ordinary arrangement for producing a series of tetanizing discharges *d*, another arrangement for modifying the relative intensities of the opening and closing discharges

nearly parallel (when they are perpendicular to each other, no line of force passes from the first to the second, and there is no induction).

Solenoids.—A battery circuit is an elementary solenoid, that is to say, reduced to a single spiral turn : like the solenoid, it is assimilable to a magnet, but to one extremely flattened out and having a north and a south pole situated, very near to each other, on the axis of the circuit on each side of the plane which contains it. Traversed by a current and free to move, such a system (closed battery floating on water) would orientate itself as a magnet, directing its axis in the magnetic meridian. A solenoid is formed by an isolated conducting wire, rolled on itself a certain number of times ; the spiral turns form

a series of circular and spiral currents. A coil, such as that of an induction apparatus or of a galvanometer, is a solenoid.

Magnet.—A magnet may be compared to a solenoid formed by molecular currents orientated like that of the spirals of a solenoid in a determinate manner; it is provided with lines of force which, starting from one pole (the north pole for example), proceed to diverge in the magnetic field (surrounding space), bend more and more, and finally concentrate themselves at the opposed pole (south pole), then, returning in the opposite direction (from the south to the north pole) in the interior of the magnet, complete the circuit. A solenoid may replace a magnet, and reciprocally, in many circumstances.

(a) *Permanent Magnet.*—A magnet which maintains its magnetization (except for slow loss) is called permanent.

(b) *Temporary Magnet.*—The superiority of the solenoid arises from the fact that it is possible to suppress or to return to it at will its essential properties, by breaking or making the electric current which supplies it: this is a temporary magnet.

(c) *Electro-magnet.*—If in a solenoid, a rod of soft iron (or a bundle of soft iron wire) is placed, the lines of force are absorbed in large numbers by the metal, which is magnetically more permeable to these lines of force than is the surrounding space; during the passage of the current a very powerful field of force is created as regards the poles by the orientation of the molecular currents of the soft iron; when the current is broken, this arrangement comes to an end, and the lines of force disappear. An electro-magnet is a temporary magnet, but more powerful than the ordinary solenoid.

Magnetization and induction are two very different phenomena. In magnetization, there is simply a special arrangement of currents, which circulate, *without any resistance*, in the molecules of the steel (permanent magnet) or of the soft iron (temporary magnet); these molecules play the part of perfect conductors. In induction, at the instant of augmentation or of diminution of the lines of force in the magnetic field, there is the same impulse and movement of electricity in the secondary circuit; but this movement, arising in an imperfect conductor, is soon arrested by the resistance of the circuit and ceases when the primary current has assumed its permanent condition or is itself arrested.

D. Stimulating Apparatus

The electric waves which are made use of for stimulation are furnished by different apparatus.

Condenser.—If a nerve is electrically connected, on the one hand with a charged condenser, on the other with the earth, the *flow of the discharge* produces a wave capable of stimulating it. It may also be stimulated by placing it in the *flow of discharge*. The discharge and the charge form two waves which are nearly equal in intensity and duration. There are different means of causing these two conditions to vary, but the shape of the wave is not well known.

The charge and the discharge depend on the resistance R, on the capacity C and on the self-induction L of the line.

For $R > \sqrt{\frac{4L}{C}}$ the discharge is continuous.

For $R < \sqrt{\frac{4L}{C}}$,, ,, ,, oscillating.

With ordinary wires which are not rolled up self-induction is a negligible quantity.

Induction apparatus.—The induced current which takes origin in the secondary coil of the apparatus of du Bois-Reymond is very usually employed for the

purpose of electrical stimulation. The two induced currents, the one inverse on closing the circuit, the other direct on opening it, are equal in quantity, but inversely unequal in duration and intensity. Self-induction considerably prolongs the first, especially if a rod of soft iron is placed in the coil. The intensity is graduated (but imperfectly) by causing the distance of the two coils to vary on a graduated scale. The intensity of the induced current decreases as the square of this distance.

Batteries ; accumulators.—Practically there is scarcely any means which is at the same time easy and correct of eliminating, in a continuous current, waves of the character of those which will be described farther on in connexion with the law of excitation. The wave of making the current is made use of, and also that of cessation (breaking of current). The action of the second is greatly complicated by the effects (electrolytic amongst others) which are due to the passage of the current.

Rheotomes.—In order to make or break the current, different apparatus may

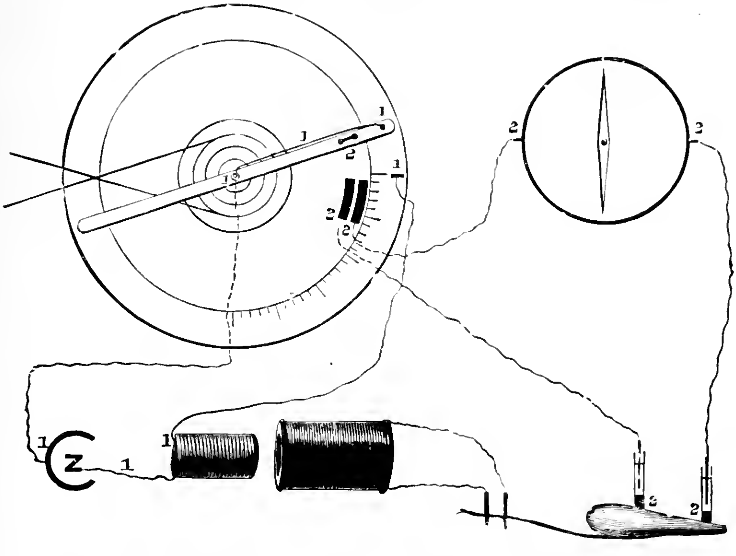


FIG. 26.—Rheotome of Bernstein (application of the method of Guillemin).

A rod which carries a contact 1 closes periodically (by a rotatory movement of the axis which supports it)—a battery circuit inducing a current which stimulates the nerve.—Further, another contact 2 (in the shape of a bridge) closes, in a galvanometer, another circuit, in which the muscle is included, and allows of the determination of the electromotor phenomena which arise in the latter from the fact of stimulation.

The contacts 1 and 2 may be mutually displaced so that (for a given rate of rotation) the interval of time which separates them may be increased or diminished. In this way the direction and the successive intensities of the electromotor phenomenon which is developed in the muscle in the period succeeding the stimulation may be studied.

be made use of, oscillating pendulums (Chauveau), contacts effected by a rotatory movement (Bernstein), which bring about these closings and openings of the circuit at equal intervals and at the same rate.

E. Apparatus for the Estimation and the Measurement of Electromotive Phenomena

Galvanometers and electrometers are employed, chiefly the electrometer of Lippmann.

Galvanometers.—Two currents, two solenoids, two magnets, one solenoid and one magnet are capable of reacting the one upon the other. If one is fixed and the other movable, when the current passes through the solenoid displacements ensue which may be made use of to prove the existence of such a current, to determine its direction and to estimate its intensity.

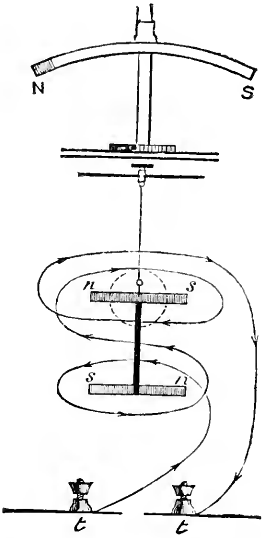


FIG. 27.—Diagram of an astatic galvanometer.

The current brought to the two terminals *t*, *t* is conveyed by a wire which is rolled successively and in contrary directions round two conjoined magnets *sn* and *ns*, forming a movable suspended arrangement. The upper magnet carries a mirror on which a luminous ray is reflected, forming an image on a graduated scale—the displacement of the image measures the intensity of the current.

N S, fixed magnet intended to give a position of repose, which can be varied at pleasure, to the two others.

Electrometer of Lippmann.—This consists of a tube ending in a conical capillary point ; it is filled with mercury, and dipped in a solution of sulphuric acid which itself rests on mercury ; when this apparatus is traversed by a current, the capillary constant is changed and the mercury is displaced in the conical point to a certain extent which varies according to the direction of the current. The amount of the displacement (within certain limits) indicates the difference of the potential.

Non-polarizable electrodes. — The contact of metallic wires with the tissues gives rise to polarizations which set up contrary currents capable of seriously invalidating observations. These difficulties may be avoided by making use of non-metallic electrodes, which are almost incapable of polarization.

D. LAWS OF ELECTRIC STIMULATION

1. The problem to be resolved.—Electricity acts as a stimulus on every excitable organ, especially on a nerve when it passes through it in the form of a current, whatever may be the nature of this latter. It only exerts its stimulating and impulsive effect so far as it is itself in movement.

A current has of necessity a period of inauguration (*a variation which is more or less rapid* in its intensity starting from zero), a phase of persistence in certain conditions (constancy of the current), a phase of cessation (of more or less rapid variation the converse of the first).

It has at every instant a determinate *intensity;* it has a *total duration;* it represents a *quantity of electricity* supplied, and it represents an *energy expended.* Which of these factors takes part in the stimulation in an exclusive or preponderant manner ?

Historical ; facts and opinions.—These questions have offered themselves for solution from the very commencement of methodical studies concerning the effects of electricity on the nerves and other excitable tissues. The researches commenced by a work of du Bois-Reymond (1848).

Experiment.—A nerve is traversed by a current; at the making of the latter a contraction of the muscle ensues; duing the passage, the organ remains in

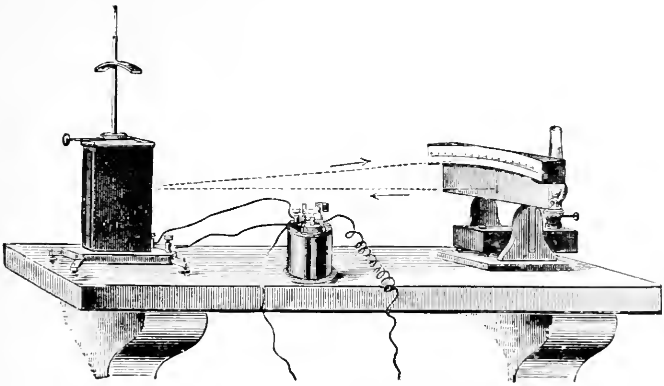


FIG. 28.—Reflecting Galvanometer with its scale for reading the deviations.

A shunt is interposed between the galvanometer and the source of the current to be measured.

repose; at the breaking of the current, there is once more a contraction. Another fact of the same kind: a nerve is included in the circuit of a battery (by the

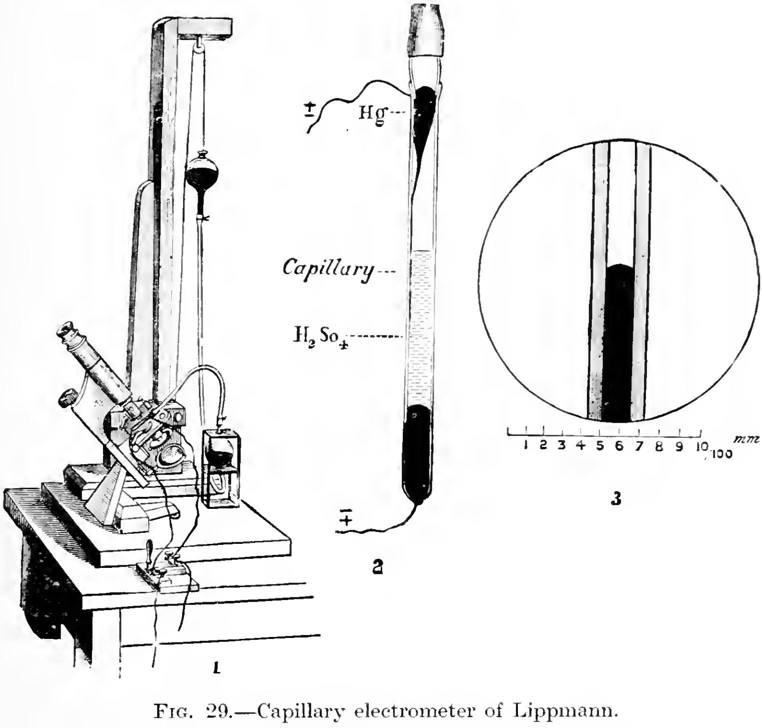


FIG. 29.—Capillary electrometer of Lippmann.

On the left, the apparatus as a whole; in the middle, diagram of the apparatus; capillary tube full of mercury plunged into a solution of sulphuric acid resting on a layer of mercury. On the right, appearance of the capillary column at its extremity seen in the microscopic field.

aid of a rheocord); the intensity of the current is caused to vary *slowly*, so that its strength may be greatly increased : there is no stimulation ; but, if a *sudden variation* is caused in the intensity of the current, there is contraction.

2. Old formula.—From this du Bois-Reymond has concluded that *it is not the absolute value of the intensity, but the variation of the intensity of the current which causes the stimulation ;* in other words : if two

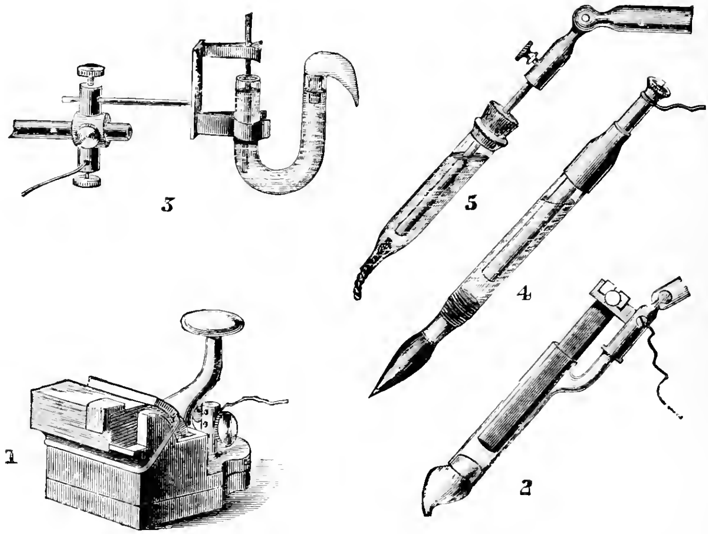


FIG. 30.—Non-polarizable electrodes for receiving the currents of muscles or nerves.

1 and 2, those of du Bois-Reymond ; 3, those of Burdon-Sanderson ; 4, those of V. Fleischl ; 5, those of d'Arsonval.

The metallic wire, contact of which with the living tissues must be avoided, is plunged into a tube filled with a solution of a salt of the same metal (zinc in sulphate of zinc, copper in sulphate of copper). The extremity of the tube is closed by a stopper of kaolin impregnated with a neutral solution of chloride of sodium and is of form suitable for application to the nerve or the muscle.

identical nerves are traversed by two currents I and I^1 which differ considerably, and if these two different currents are made to increase or decrease by the same quantity, during the same time and in the same manner, the two nerves will be equally stimulated. The stimulation will be so much the greater as the variation dI in the unit of time is greater, that is to say, the variable period is more rapid, the wave shorter.

Contradictory facts.—It was thought at first that the experimental fact on which this theory of stimulation is based was of general application. In reality this is not the case. In operating on other animals, it may be found wanting. Grutzner (1887) has observed that the motor nerve of the toad responds better to slow and prolonged variations of the current than to those which are rapid. Fick finds that, even in a frog, a muscular response is not elicited when the passage of the wave is of very short duration. Brucke finds that it is the same as regards

curarized nerves, so long as the poisoning lasts. Pflüger observes that nerves react, in certain conditions, even to a constant current. Hence it cannot be admitted that the variation of intensity is the sole and only factor of the stimulation.

Cybulski and Zanietowski, as also Waller, consider that the important factor is the electrical energy. But Boudet (of Paris) had previously found that " the same quantity of electrical energy expended did not always produce the same effect."

Fick (1869) and Wertheim-Salomonson attribute a direct influence on the magnitude of the reaction to the quantity of electricity, but without regarding it as the sole factor in stimulation.

G. Weiss (1901) has re-investigated the subject by the aid of very exact methods, and he proves that the quantity of electricity made use of is the important factor in electrical stimulation.

3. **Conditions which must be observed ; method.**—A wave of a simple form must be capable of being projected into a nerve, and the duration, as also the intensity of this wave, must be exactly known. Acquainted with the duration, as well as with the intensity, it will be possible, in the preliminary discussions, to determine the threshold of excitation, that is to say, the intensity which, for a given duration, is just sufficient to cause a contraction. Having thus determined the wave which gives the threshold of excitation, an abbreviation of this is effected in such a manner as to reduce somewhat its duration, thus forming two waves of a total duration which is less than that of a standard wave. Contraction no longer results (or, the conditions being the same, in order to obtain it, the voltage must be increased). If the stimulation were due to the variation of the potential, conformably to the hypothesis of du Bois-Reymond, contraction should have taken place. If two waves of a total duration equal to that of the standard wave are projected into the nerve, contraction follows.

Result.—Thus it is clearly seen that, *in every case, it is the quantity of electricity which is here the important factor, and not the energy*, for the latter may be equal for a lesser, or greater for an equal quantity, without any change in the results.

Apparatus.—For the purpose of having at command an electric wave of a known intensity and duration which has been accurately determined, the majority of the apparatus employed (condensers, induction coils, etc.) are worthless. G. Weiss has invented the following arrangement, which is altogether satisfactory.

(a) *Estimation of the Duration.*—The nerve is interpolated in the circuit of a constant battery. This circuit contains a derivation of a relative resistance such that (as regards the wires going to the nerves), all being entirely closed, the nerve receives no appreciable quantity of electricity. If, then, the derivation is broken at a point, the current passes into the nerve ; if the interruption occurs at a second point, this time in the circuit, the current ceases to pass, the wave is finished. Its duration is measured by the time which elapses between the two

interruptions. These interruptions are effected by the ball of a carbine worked by liquid carbonic acid, whose rate is 130 metres a second (at the temperature of the laboratory).

The interval between the two interruptions depends on the distance between the wires, the latter being placed parallel to one another in the plane of transit of the ball. For an interval of one centimetre, the duration of the wave will be $0^{sec},000077$, etc.

By making the arrangement more complicated, several successive waves may be obtained having definite durations, succeeding one another at definite intervals of time, so that the comparisons and controls indicated above may be effected. Such is the mode of estimating the duration of the wave.

(b) *Estimation of the Intensity.*—To calculate the intensity, the voltameter is connected with the terminals of the battery or the distributer of the potential. This voltameter registers a figure proportional to the intensity of the current, since in the successive experiments the resistance of the circuit does not vary ($E = IR$; $E^1 = I^1 R$; EE^1 is proportional to II).

If the value of current is not determined with absolute precision, yet it is so within very narrow limits.

(c) *Ratio of the Energy to the Quantity.*—The energy of the current is expressed:

$$EIt = E^2t \times R.$$

It is, as a constant factor, nearly $W = E^2t$.

The quantity of electricity employed is $Q = It = Et \times R$.

It is, as a constant factor, nearly $Q = Et$.

It is seen that the quantity of electricity varies as E, while the energy varies as its square, E^2.

For a given duration the quantity remains constant.—Thus the first stage of the argument is established. *For a given period of time, in order to obtain the threshold of excitation, the same quantity of electricity is required.* If this necessary quantity is not supplied to the nerve, the minimum excitability is raised. This minimum is so much the more elevated as the frequency of the wave is greater, that is to say, shorter. When the frequency is sufficiently great, very high voltages may be employed without attaining the threshold of excitation.

The threshold of excitation implies, for a given duration, a given quantity of electricity. Supposing that the duration varies, will this quantity remain fixed or will it vary, and if so, how ?

Variation of the quantity as a function of the duration.—From the formula $Q = Et$ it is obvious that a quantity of electricity remains the same if its two factors, intensity and duration, undergo proportionally inverse modifications. Will the same threshold of excitation be maintained if t and E are modified inversely, in such a manner as to preserve Q equal to itself ? Experience tells us that this is not so.

In proportion as the duration t augments, the quantity Q augments equally. This shows that the quantity Q represents the sum of two terms, the one fixed, which may be described as A, the other B, proportional to the duration of the excitation. Hence the quantity required to produce the excitation becomes : $Q = A \times Bt$.

In order to prove this, a series of initial stimuli are applied to the same nerve in identical conditions, the waves being of variable duration but not exceeding 0^{sec} 0023, while at the same time in each case the quantity of electricity is measured. The duration of the wave (time of stimulation) is represented by

abscissæ ; the quantity of electricity employed is expressed in ordinates. Thus is obtained a straight line which does not pass through the origin. It represents the quantity of electricity which is required for the minimum excitation of the nerve expressed as a function of the duration of the stimulation.

4. **Law of electrical stimulation.**—The researches of G. Weiss explain the paradoxical facts of Grutzner, of Brucke, and, further, they lead to a general law which is applicable at the same time to the more prompt reaction of the nerve of the frog. This is in accord with the results of Dubois (of Berne) and of Horweg, which were obtained in making use of the condenser. The law may be thus expressed : *In order to obtain the initial response of a nerve or of a muscle, electrical stimulation must make use of a constant quantity of electricity ; and, further, this quantity must be proportional to the duration of the discharge.*

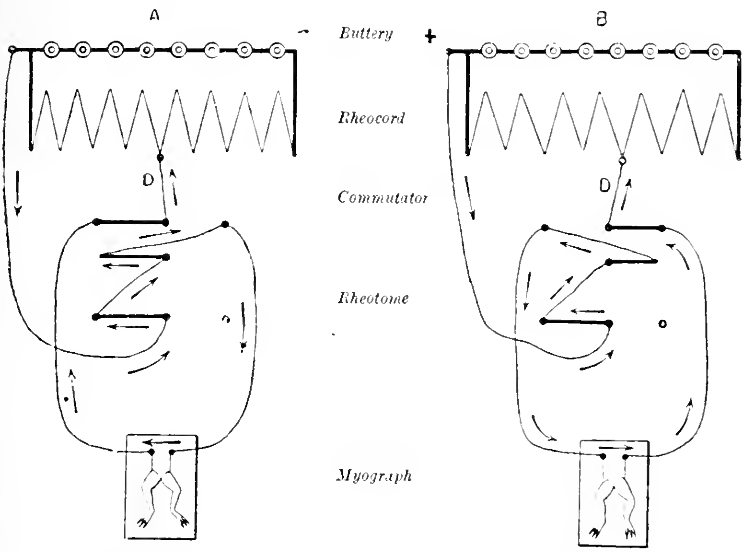


FIG. 31.—Arrangement for the stimulation of nerves. Action of the constant current.

According to this observer, " everything tends to prove that a constant quantity of electricity is necessary in order to stimulate a nerve, but that it is also necessary, during the whole of the operation, to ceaselessly oppose a process of return to the first state by means of another quantity of electricity which is proportional to the duration of the action."

5. **Methods of stimulation.**—In order that the nerve may be stimulated by a current, matters are so arranged that the nerve forms part of the circuit traversed by this current, at least for a small portion of its length.

According to circumstances, two arrangements are made use of. In the one the isolated nerve is placed in contact with the two electrodes, which are situated at a certain distance the one from the other. The lines of passage of the current follow the direction of the nerve as in a regular cylinder ; the density of the current is the same at its entrance, at its exit and in the intervening space : this is the *bipolar method*. In the other, the nerve, usually superficial, but adherent to the mass of subjacent tissues, is in contact (often through the skin) with one of the two poles, the other pole being placed at some distance.

The lines of transmission, if the positive pole is on the nerve, diverge

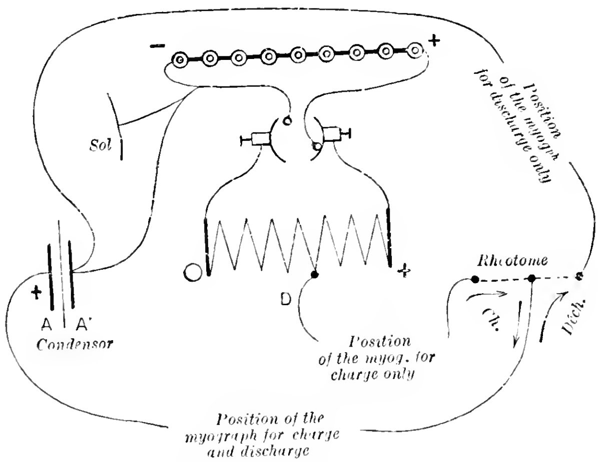


FIG. 32.—Arrangement for the stimulation of nerves. Action of the charge and discharge of the condenser.

from the point of contact in every direction and proceed to complete the current at the other pole : or, if the negative pole is on the nerve, converge parallel to the nerve starting from the positive pole : this is the *monopolar method*.

Polar influence.—This second arrangement, designed and recommended by Chauveau, shows in a very definite manner *the different action of the two poles.* Let it be assumed that the two electrodes are symmetrically placed on two similar nerves, as the two facial nerves in mammals or the sciatic nerve in the frog, and let the current be projected alternately in the two directions. *As the intensity of the current increases from zero, the first contraction will occur in connexion with the negative pole*, whether it is on the right or on the left, while the muscle in contact with the positive pole will remain in repose. *When the strength increases, starting from this point, a new threshold of excitation arises for the positive pole ; then the contractions become equal ; later,*

those at the positive pole become predominant, while those at the negative pole tend to diminish. Finally, according to Boudet (of Paris), if the intensity still increases, the contractions at the positive pole diminish in their turn, once again become equal to those at the negative pole, then diminish more rapidly than these last, and cease before them.

The effects due to each of the two poles may be represented by two curves, the one more extended and more elliptical (negative pole), the other shorter and with a still higher summit (positive pole) which present two points of intersection.

Active pole; indifferent pole.—In electro-therapeutics, it is not generally necessary to stimulate the two nerves symmetrically and alternately; usually a single nerve is alone treated.

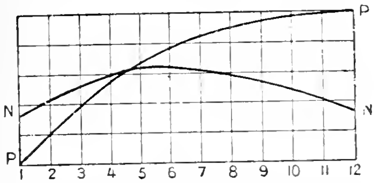


FIG. 33.—Inequality of the polar actions of the current (after Chauveau).

N N, curve representing the values of the contractions of the negative pole on the making of the current. P P, curve of the contractions of the positive pole. Equality at the point of intersection of the two curves; inequality of opposite nature before and after it. 1, 2 . . . 12, successive intensities of the stimulating current.

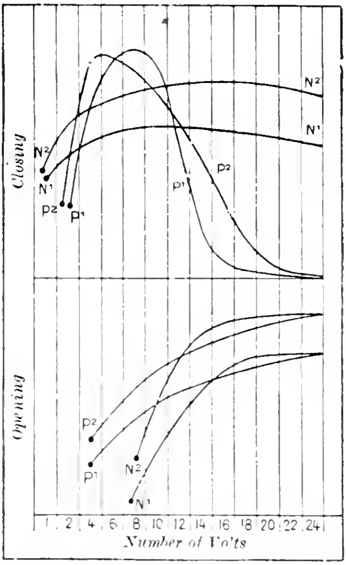


FIG. 34.—Inequality of the polar actions (after Boudet, of Paris).

The effects of closing and opening are examined separately in two experiments. N^1 N^2, negative pole; P^1 P^2, positive pole.

The electromotor force of the current increases from 1 to 24 volts.

Thus the pole whose action is required is placed on the nerve, and on another locality situated at some distance, and but little sensitive, is placed the other pole, which is known as *indifferent*, and which covers a large surface (moistened sponge).

Cathode; anode.—The negative pole is usually known as the *cathode* (in the case of a feeble current this is the most active), and *anode* describes the positive pole (in the case of a strong current this is the most active).

Direction of the current.—In the bipolar method, the lines of transmission of the current are projected, according to the direction of the nerve, alternately in two opposite directions, that is to say, according to the direction of its conduction (*descending* current) or in the opposite direction (*ascending* current).

The effects differ in the two cases. Contrary to what might have been thought, the differences are not due to an influence attributable to the physiological conduction of the nerve, but once again to a polar influence. It is seen, indeed, that the results are inverted, as above, according to the intensity of the current, and that they follow fundamentally the same law as in monopolar excitation. It is sufficient, in order to recognize it, to remark that, in the case of bipolar stimulation with the descending current, the lines of flux have the same orientation as in monopolar excitation with the negative pole on the nerve; and the same with the ascending current in the bipolar excitation, the same also with the positive pole in monopolar excitation.

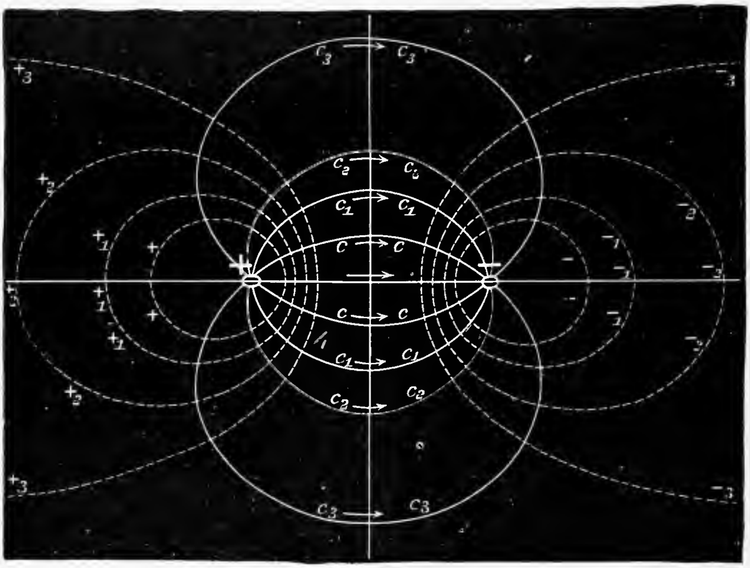


Fig. 35.—Diffusion of the electric current in a homogeneous conducting medium, diagram of the points of application of the two poles.

The current is completed by *lines of flux* of which one only is straight, the others are inflected to a greater or lesser extent, c, c_1, c_2, c_3, and represent the derivations of the current, feeble in proportion as they are further removed from the direct course.

These lines are cut by the *equipotential lines* (represented in strokes) $+$, $+_1$, $+_2$, $+_3$; $-$ $-_1$, $-_2$, $-_3$.

These lines connect the points of the conducting medium having the same potential, the same positive tension to the right, negative to the left of a line of zero potential, which cuts perpendicularly the straight line uniting the two poles.

Unipolar stimulation in an open circuit.—When the two poles of the stimulating circuit are placed on the same nerve, the stimulation is called bipolar. When a single pole is placed on the nerve, the other pole, covering a large surface, being placed on a remote region of the animal's body, then it is a case of monopolar or unipolar excitation, such as has been recommended by Chauveau, and is ordinarily made use of in electro-therapeutics. But a nerve may also be stimulated in a unipolar manner by a different method of procedure. For example, on the one hand the indifferent pole, on the other the body of the animal experi-

mented on, may be connected electrically with the earth. This method is closely related to the preceding; it differs from it inasmuch as the earth is interposed in the circuit. Lastly, after having isolated both the animal and the distributer of energy, communication may be established through a single pole with a nerve of the animal, and in this way, again, motor effects may result.

The efficacy of this kind of stimulation which, at the first glance, would appear to be *nil*, is, as a matter of fact, tolerably great. In this case, as in all the others, *the stimulation is due to a movement of electricity in the tissue (the nerve) which is connected with the active pole.*

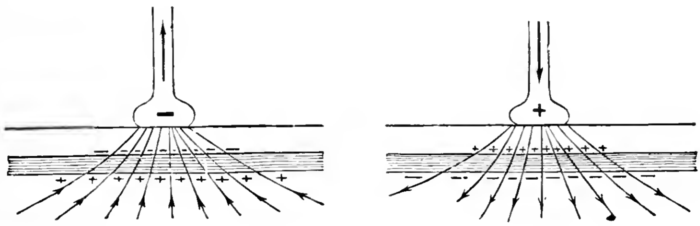


FIG. 36.—Diagram showing the internal polarization of the tissues (after Waller).

All along the lines of the flow of the current, going from one pole to the other, secondary polarities are developed across the heterogeneous portions, traversed by electrolytic conduction.

When, indeed, an induction shock is produced, if the induced current is open a more or less large number of electrical oscillations are produced, whose frequency depends on several conditions, and more especially on the capacity of the system (Schiller and Mouton). This frequency amounts to 10,000 a second. The currents furnished by this unipolar stimulation are then alternately positive and negative, or diphasic currents, persisting a longer or shorter time according to circumstances.

A. Charpentier has methodically studied the action of these special currents (*Archives of Physiology*, 1893-1896).

Periodic excitations.—So far we have assumed a simple stimulation due to an isolated wave. But, in practice, when, instead of studying the laws of stimulation, it is merely desired to make use of the latter in order to demonstrate the functions of a given nerve, the excitation is prolonged and renewed in the nerve by the passage of a periodical series of similar waves which succeed one another inversely. This effect is realized by means of the *trembleur* of du Bois-Reymond's apparatus. These currents are called *tetanizing*, because the muscular contractions which follow them in the muscle are so close together that they unite themselves in producing a *physiological tetanus* by which the tension of the muscle is maintained.

In man, the object of the stimulation is not the determination of function, but the forming of a diagnosis or the production of a therapeutic action on the nerve. In animals it is the reverse. In the first case, the monopolar method is the only one applicable, and is very convenient; in the second the bipolar method is sometimes preferable, because it permits of the stimulation being localized on a given nerve. Usually the nerve has been cut and is supported on the electrodes of the current by the aid of a white silk thread which is very dry: in this way all danger is averted of the derivation of the current to excitable parts other than the nerve under investigation.

Remark.—Elsewhere we have assumed that the stimulus is applied to a nerve element or to a bundle of nerve elements of similar functions, which thus together form a simple object. In practice this is rarely the case. The nervous bundle

which is stimulated will frequently contain parallel elements which terminate in peripheral organs having distinct functions, which the excitation will to a certain extent dissociate by revealing their presence. Sometimes, indeed, the bundle will contain antagonistic elements, for example, a mixture of motor and inhibitory elements, to such an extent that the action which ensues will be the resultant of two contrary actions. The effect produced in this case no longer measures the excitability of a given nerve, but something much more complicated. It is probably for this reason that the excitability of the great sympathetic and of other analogous nerves, that of the tracts of the spinal cord and of the different portions of the brain, seems to be less than that of the peripheral motor nerves of the skeletal muscles ; these last are the only really simple nervous structures on which we can act.

BIBLIOGRAPHY

Nerve Elements.—Apathy, *Mittheilung. aus der Zool. Stat. zu Neapel*, vol. LII, 1897.—Arnold, Struct. und Architect. d. Zellen, *Arch. f. mikr. Anat.*, vol. LII, 1898.—Auerbach, *Neurol. Centralbl.*, vol. XVII. 1898 : *Monatschr. f. Psych. und Neurol.*, vol. IV, 1898.—Berder, La cellule nerveuse, thèse d'habilitation, Lausanne, 1893.—Bethe, *Arch. f. mikr. Anat.*, vol. L, 1897 ; *Anat. Anz.*, XIV, suppl., 1878 ; *Morphol. Arbeit. v. Schwalbe*, VIII, 1898 ; *Neurol. Centralbl.*, XVII, 1898.—Deiters, Unters. üb. Gehirn und Rückenm., Braunschweig, 1865.—Bidder et Kupffer, Untersuch. üb. die Text. d. Rückenmarks, Leipzig, 1857.—Dogiel, *Arch. f. mikr. Anat.*, Bd. XLVI, 1895.—Dohrn, *Mitth. d. Zool.* Naples, 1891 ; *Anat. Anz.*, 1892.—Flechsig, Die Leitungsbahn. im Gehirn und Rückenm., Leipzig. 1876 ; Entwicklung . . ., *Arch. f. Anat. und Entwick.*, 1881, p. 12.—Forel, Einige hirnanat. Bechtr. und Ergebn., *Arch. f. Psych. und Nervenkrank.*, Bd. XVIII, 1887.—Garbowsky, Doctrine d'Apathy, *Biol. Centralbl.*, 1898.—Gerlach, Article "Rückenmark" *in* Stricker's Handb., Bd II, 1871.—C. Golgi, Sulla fina struttura d. bulb. olfatt., Reggio Emilia, 1875 ; Localis. cérébrales *Arch. ital. de biol.*, 1882 ; Rech. sur l'histol. des centres nerveux, *Ibid.*, t. III, 1883, t. IV, 1883, t. VII, 1886 ; Sulla fina anatomia degli organi centrali del syst. nerv., Milan, 1886 ; Rückenmark., *Anat. Anz.*, 1890 ; La rete nervosa diffusa degli organi centrali del syst. nervoso, suo signifaeato fisiologico, *Rend. del R. Istit. Lombardo*, 1891 ; Gangl. spin., *Bull. Soc. méd. chir. Pavie*, 1898 ; *Arch. ital. de biol.*, vol. XXX, 1898 ; Struct. cell. nerv., *Gaz. med. lomb.*, L. VII ; Termin. nerv. intracell., *Arch. ital. de biol.*, vol. XXX.—His, Histogenèse et connex. des élém. nerv., *Arch. f. Anat. und Physiol.*, suppl., vol. VII, 1890 ; *Berlin. klin. Wochenschr.*, 1893.—Kölliker, Handbuch . . . Leipzig, 1893 ; Bulb. olfact., *Sitz. d. Wurburg. Phys. med. Gesellsch.* 1891.—V. Lenhossek, *Anat. Anz.*, 1890 ; *Correspondenzbl. f. Schweiz. Aerzte*, 1891 ; *Forschritte der Medicin*, 1892 ; *Arch. f. mikr. Anat.*, Bd. XXXIX, 1892 ; Spinalgangl., *Beitrage zur Histol. des Nerv. Syst. und Sinnesorgane*, Wiesbaden, 1894.—Leeuwenhoek, Opera, t. II, p. 351.—Martinotti, *Internat. Monatschr. f. Anat. und Phys.*, Bd. VII, 1890.—Monti, Signif. physiol. des prolong. protoplasm. des cell. nerveuses, *Arch. ital. de biol.*, t. XXIV, 1895.—Nansen, Die Nervenelemente . . ., *Anat. Anz.*, 1888.—Pierret, Relations existant entre le volume des cellules motrices ou sensitives des centres nerveux et la longueur du trajet . . ., *C. R. Acad. sc.*, 1878.—Ramon y Cajal, *Revista trimestrial de histologia normal y pathologica*, 1888–1889 ; *Internat. Monatschr.*, Bd. VI, Heft 3 et 4, 1889 et 1890 ; *Anat. Anz.*, 1890 ; *Gaceta sanit. d. Barcelona*, 1890 ; Encéphale des reptiles, Barcelone, 1891 ; Les nouvelles idées sur la structure du système nerveux, Paris, Reinwald et Cie, 1896 ; *Revue trimestr. de micrographie*, 1896–1898.—P. Ramon, *Gaceta sanit. de Barcelona*, 1890. —Ranvier, *C. R. Acad. sc.*, et *Arch. physiol.*, 1871 ; Leçons sur l'histologie du syst. nerveux, Paris, Savy.—Schaffer, The nerve cell considered as the basis of the Neurologie, *Brain*, 1893.—Van Gehuchten, in *La cellule*, 1891 et 1892 ; Anatomie du système nerveux, *Bfbl. anatom.*, 1899 ; Lobe olfact. de l'homme, Paris, Levrault, 1895.—Van Gehuchten et Nelis, Gangl. spin., *Bull. Acad. roy. méd. Belgiq.*, 1898.—Verrati, *Anat. Anz.*, vol. XIII et XV.—Vignal, Développement . . . *Arch. physiol.*, 1884 et 1888 ; *C. R. Acad. sc.*, 1886.—Waldeyer, . . . Neure Forschungen . . . Central Systeme, *Deut. medic. Wochensch.*, 1891. Traduit en français par Devic, *Province médicale*, 1893–1894.

Connexions of fibres and cells.—Cajal, *Journ. de l'anat. et de la physiol.*, 1896.—Dogiel, *Anat. Anz.*, vol. XXXIII. 1896.—Donaggio, *Rivista sperim. di frenatria*, XXIV

2, 1898.—Golgi, *Arch. ital. de biol.*, vol. XXX; *Rend. R. Istit. Lomb. di sc. e litt.*, vol. XXXI, 930.—Lenhossek, *Biol. Centralbl.*, 1898, vol. XVIII, p. 843; *Neurol. Centrabl.*, 1899; *Revue neurol.*, 1899.—Mann, *Anat. Anz.*, suppl., 1892.—Martinotti, *Annali di frenatria*, vol. IX, 1899.—Ranvier, Des tubes nerveux en T et de leurs relations avec les cellules ganglionnaires, *C. R. Acad. sc.*, 2 fév. 1875; Sur les ganglions cérébro-spinaux, *Ibid.*, 4 déc. 1882.—Redligh, *Bull. méd. Paris*, 1895.—Waldeyer, *Abh. d. k. preuss. Akad. d. Wissen. zu Berlin*, 1888–1889.

Structure of the nerve fibres.—Frommann, *Virchow's Archiv.* 1864, t. XXXI, p. 151.—Lanterman, *Arch. f. mikr. Anat.*, 1876.—Mauthner, *Acad. des sc. de Vienne*, t. XXXIX.—Purkinje, Encyclop. anat., t. VII, p. 348.—Ranvier, *C. R. Acad. sc.*, 1871, et *Arch. de physiol.*, 1871; Leçons sur l'histologie du système nerveux; Traité technique d'histologie.—Remak, *Froriep's Neu Notizen*, No 47, 1837.—Schmidt, *Monthly Microscopic Journal*, 1874.—Schwann, Microscop. Untersuch., p. 174; *Encyclop. Anat.*, t. VII. p. 347.—Waldstein et Weber, Études histochimiques, *Arch. de physiol.*, 1882, 2ᵉ série, t. X.

Specificity of the neurons.—Demoor, *Journal médical de Bruxelles*, No. 38, 1897; *Arch. de biol.*, t. XIII et XIV.—Heger, *Trav. Instit. Solvay*, fasc. III.—H. Held, *Arch. f. Anat. und Physiol.*, Anat. Abth., 30 juillet 1897.—Kölliker, *Handbuch der Gewebelehre*, 1896.—Lenhossek, Der feinere Bau des Nervensystems, Berlin, 1897.—Fr. Nissl, Die Hypothese der specifisch. Nervenzellenfunct., *Allg. Zeitsch. f. Psychiatr.*, Bd. CCLXI et 2 Heft, 1897.

Dynamic polarization.—Lugaro, *Monitore zoologico ital.*, an VIII, 1897.—S. Ramon y Cajal, *Rev. trimestrial micrografica*, 1897, II.—Van Gehuchten, Syst. nerveux de l'homme, 2 édition, 213.

Nervous amœboism.—Azoulay, *Année psychologique*, 1896.—J. Demoor, Plasticité des neurones, mécan. et signif. de l'état monilif. des neurones, *Trav. Instit. Solvay*, t. II, fasc. I, 1896 et 1898, et *Arch. de biol.* de Bruxelles.—R. Deyleer, État actuel de la question de l'amiboïsme nerveux, Paris, 1896.—Mathias Duval, L'amiboïsme des cellules nerveuses, *Revue scient.*, 1898, p. 329; *Soc. de biol.*, 2 fév. 1895; Précis d'histologie, Paris, Masson, p. 971.—J. Havet, État monilif. des neurones chez les invertébrés, *La cellule*, t. XV, fasc. I, 1899.—Lépine, Sur un cas d'hystérie à forme particulière, *Revue de médecine*, 1894, p. 713.—Lugaro, Modific. morfolog. funzional, *Rivista di Pathol. nervosa*, 1896 et 1898.—Manouélian, *Revue scientif.*, 1898, p. 328; *Année psychol.*, 1898, p. 439.—Morat, *Biol.*, 1895.—Robert Odier, Rech. expér. sur mouv. cell. nerv., Genève, 1899.—Pergens, Action de la lumière sur la rétine, *Ann. Soc. roy. sciences méd. et nat. de Bruxelles*, t. V, fasc. III, 1896.—Ch. Pupin, Le neurone et les hypothèses histologiques sur son mode de fonctionnement; théorie histologique du sommeil, Paris, 1896.—L. Querton, Sommeil hivernal mod. des neurones, *Trav. lab. Instit. Solvay*, t. II, fasc. I, Bruxelles, 1898.—Rabl-Rückard, Sind die Gangl. zell. amib., *Neurol. Centralbl.*, p. 199, 1890.—M. Schultze, *Stricker's Handbuch*.—Stefanowska, Append. terminaux des dendrites, *Trav. lab. Instit. Solvay*, fasc. III, Bruxelles, 1897.—Tanzi, *Rivista speriment. di frenat. e di medicina legale*, vol. XIV, fasc. II–III, p. 419.

Metabolism of the nerve: acidity during functional activity.—Boll, *Arch. f. Physiol.*, Leipzig, 1873, s. 99.—Funke, *Centralbl. f. die med. Wissensch.*, Berlin, 1868.—Heidenhain, *Centralbl. f. die med. Wissench.*, Berlin, 1868.—Fühne, Causation of vital movement, Croonian Lecture, 1888, *Proc. Roy. Soc.*, London.—Marcuse, Inaug. Dissert., Breslau, 1891.—Röhman, *Arch. f. Physiol.*, Leipzig, 1893, s. 423.—Waller, Croonian Lectures, *Philos. Trans.*, London, 1896.—Weyl, *Arch. f. Physiol.*, Leipzig, 1893, supplém. s. 109.

Heating.—(Voy. *Chaleur animale*).—Heidenhain, *Stud. d. physiol., Inst. zu Breslau*, 1868.—Hill et Nabarro, *Journ. of Physiol.*, Cambridge and London, 1895.—Mosso, Die Temp. des Gehirns, Leipzig, 1894.

Degenerations: Wallerian degeneration: structural alterations.—Arloing, *Biol.*, 1886.—Eichort, *Arch. de Wirchow*, 1873, t. LIX, p. 1.—Engelmann, *Arch. f. die ges. Phys.*, 1876, t. XIII, p. 480.—Eulenbourg et Landois, *Berlin. klin. Woch.*, 1865, Nos. 45 et 46.—Fontana, *Ricerche filosofiche sopra la fisica animale*, Florence, 1775. (Voy. art. de Brown-Séquard in *Journ. de la physiol.*, t. II, p. 75).—Kickhepel, *Virchow's Arch.*, CXXIX.—Sent, *Zeitschr. f. Wissensch. Zool.*, t. VII, p. 145.—Mott et Halliburton, Chimie de la dégénération, *Philos. Trans.*, London, 1901.—Muller, Manuel de physiologie, traduction française, t. I, p. 351.—Nasse, *Muller's Arch.*, 1839, p. 413.—Neumann, Dégénér. et régén., *Arch. f. Heilkunde*, t. IX, 1868, p. 201.—Philipeaux et Vulpian, *Biol.*, 1859, p. 343.—Ranvier, Leçons sur l'histologie du syst. nerv., Paris, Savy, 1878; *C. R. Acad. sc.*, 1872.—Remak, *Arch. de Virchow*, 1862, t. XXIII, p. 441.—Schiff, Recueil de mémoires, *Arch. des Vereins f. gemeinschaftliche Arbeiten*, t. I.—Ströbe, *Ziegler's Beiträge*, XIII, 2, p. 160; *Centralbl. f. Physiol.*, 1893.—A. Waller, Nouvelle méthode pour l'étude du système nerveux applicable à l'investigation de la distribution des cordons nerveux, *C. R. Acad. sc.*, 1852, t. XXXIII, p. 606; Nouv. obs. sur régén. des nerfs, XXXIV, p. 393 et p. 675; Recherches expér. sur struct. et

fonct. des ganglions, XXXIV, p. 525 ; Observ. sur effets de la section des rac. spinales du nerf pneumogastrique au-dessus de son ganglion inférieur chez les mammifères, XXXIV, p. 582 ; Examen des altérat. qui ont lieu dans les filets d'origine du nerf pneumogastrique et des nerfs rachid. par suite de la section de ces nerfs au-dessus de leurs ganglions, XXXIV, p. 843 ; Mémoire sur le syst. nerveux, XXXIV, p. 979 ; XXXV, pp. 301, 561, 378.—VULPIAN, *Arch. de physiol.*, 1871–1872.

Modifications of excitability.—ARLOING, *Arch. physiol.*, 1896.—ARLOING et TRIPIER, *Arch. physiol.*, 1876.—BROWN-SÉQUARD, Rech. sur l'irritabilité musculaire, *Bull. Soc. philom.*, 1847, pp. 74 et 83 ; *Journ. anat. et physiol.*, t. II, 1859, p. 75.—LONGET, Traité de physiologie, 2 édition, t. II, p. 225.—RANVIER, Leçons sur l'histologie du syst. nerveux.—WALLER, Sur la reproduction des nerfs et sur la structure et les fonctions des ganglions spinaux, *Arch. de Müller*, 1852, p. 597.

Chromophile substance ; chromatolysis ; reaction at a distance.—BALLET et FAURE, Atrophie gr. cell. pyram. zone mot. après section des fibres de project. chez le chien, *Semaine médicale*, 1899.—DEJERINE, Chromatolyse dans infections av. hyperthermie, *Biol.*, 1879.—LUGARO, *Rivista di pathol. nervosa e mentale*, vol. I, 1896.—MARINESCO, Pathologie générale de la cell. nerv., *Presse médicale*, 1897 ; Recherch. sur hist. cell. nerv. consid. physiol., *C. R. Acad. sc.*, 12 avril 1898.—NISSL, *Tageb. der Naturforsch. zu Strassburg* 1885 . . . *zu Cöln* 1889 . . . *zu Heidelberg* 1890 ; *Allgem. Zeitsch. f. Psychiat.*, 1893 ; *Neurol. Centralbl.*, 1894, et suivants ; *Centralbl. f. Nervenheilkunde*, Jhg., 18. Ne.—ONUFROWICZ, *Journ. of nerv. and ment. dis.*, 1895.—PUGNAT, Modif. cell. nerv. fatigue, *C. R. Acad. sc.*, 8 nov. 1897.—RAMON Y CAJAL, *Revista a trimestrial micrografica*, vol. I, fasc. I, 1896.—RANVIER, Traité technique d'histologie.—DE QUERVAIN, *Arch. de Virchow*, Bd. CXXXIII, 1895.—SCHAFFER, *Neurol. Centralbl.*, 1893.—SCHWALBE, *Ienaische Zeitsch.*, Bd. X.—VAN GEHUCHTEN, *Bull. Acad. méd. de Belgique*, 1897 ; *Acad. roy. Belgique*, 1898.

Ascending degeneration.—DEJERINE et SOTTAS, *Biol.*, 1895.—DURANTE, *Assoc. avanc. des sc.*, Bordeaux, 1895 ; *Editions scient.*, Paris, 1895.—KLIPPEL et DURANTE, *Rev. de méd.*, 1895.—G. BALLET, *Congr. neurol.*, Nancy, 1896.—LUGARO, *Rivista di path. nerv. et ment.*, vol. I, 1896.—MONAKOW, *Congr. natur. all.*, Nurenberg, 1893.—MARINESCO, *Neurol. Centralbl.*, 1892 ; *Presse médicale*, déc. 1895 ; *Biol.*, 1896.—MOURATOW, *Soc. neur. et psych.*, Moscou, 1893.

Atrophy of the spinal cord after amputation.—BERG, *Thèse Paris*, 1896.—FRIEDLANDER et KRAUZE, *Forschr. d. Med.*, 1884, No 4.—HAYEM et GILBERT, *Arch. physiol. norm. et path.*, 1884, III, p. 430.—MARINESCO, *Neurol. Centralbl.*, 1892, p. 463.—REDLICH Obs. sur cobayes, *Centralbl. f. Nervenheilk.*, 1893.—VANDERVELD et HEMPTINNE, *Journ. méd. Bruxelles*, 1893.—H. WILL, *Arch. f. Psychiat.*, 1895, XXVII, p. 585.

Nervous suture ; reappearance of the functions.—BACHOWIECKI, *Arch. f. microsc. Anat.*, t. XIII, 1876, p. 420.—CALUGAREANU et VICTOR HENRI, Régénération fonction, nelle de la corde du tympan suturée avec le bout central de l'hypoglosse, *Biol.*, janvier et décembre 1901.—HERZEN, Doctrine de SCHIFF, *Rev. scient.*, 1894.—LANGLEY, *Journ. of Physiol.*, 1899, vol. XXIV.—LAUGIER, *C. R. Acad. sc.*, 20 juin 1864.—NELATON, *Soc. de chir.*, 22 juin 1864.—SCHIFF, *Rec. de mém.* ; VANLAIR, *Assoc. avanc. des sc.*, Toulouse, 1887 ; *Arch. biol. de Van Beneden*, 1893, t. XXIII ; *Rev. scient.*, 4 août 1894 ; *Ann. Soc. médico-chirurg. de Liége*, 1895.

Regeneration.—BROWN-SÉQUARD, *Biol.*, 1882.—MARINESCO, *Biol.*, 1894, p. 389, et nov. 1896.—PHILIPEAUX, Retour des fonctions du vague en trente jours, *Biol.*, 1876.

Conduction in two directions.—AMBROSOLI, Schmidt's Jahrb. 1860, p. 289.—ARLOING et TRIPIER, *Arch. f. Physiol.*, 1876.—BABUCHIN, *Arch. f. Physiol.*, Leipzig, 1877 ; *Arch. f. Anat. und Phys.*, 1877.—P. Bert, Greffe animale, *Biol.* ; *Soc. philom.* ; *Thèse de médecine*, Paris ; *Journ. anat. et physiol.* ; *Ann. sc. nat.* ; *Soc. des sc. de Bordeaux*, 1863 à 1865 ; Transmission dans les nerfs de sensibilité, *C. R. Acad. sc.*, 1877.—BIDDER, . . . lingual . . . hypoglosse . . ., *Arch. de Reichert et du Bois-Reymond*, 1865, p. 246.—FLOURENS, Syst. nerveux.—GOTCH et HORSLEY, *Philos. Trans.*, London, 1891, vol. CLXXXII, p. 485.—HELMHOLTZ, *Monatsb. d. Berl. Acad.*, 1894, p. 328.—W. KÜHNE, *Monatsb. der Kön. Akad. der Wissensch. zu Berlin*, 1859, p. 400 ; *Zeitsch. f. Biol.*, Bd. XXII, p. 305 ; *Arch. f. Anat. und Physiol.*, 1859.—LANGLEY, *Journ. of Physiol.*, 1899, vol. XXIV.—PHILIPEAUX et VULPIAN, *Journ. de la physiol. de l'homme et des anim.* et *C. R. Acad. sc.*, 1863.—ROSENTHAL, *Centralbl. f. d. med. Wiss.*, 1864, p. 449.—THIERNESSE et GLUGE, *Bullet. Acad. roy. Belgique*, t. VII, No. 7.—VULPIAN, *C. R. Acad. sc.*, 1873, t. LXXVI, p. 146 ; *Arch. physiol.*, 1876, p. 597 ; Leçons sur la physiol. gén. et comparée du syst. nerveux.

Direction of the transmission ; part played by the dendrites.—MISLAWSKY, *Biol.*, 1895, p. 489.

Rate of transmission of the impulses.—BERNSTEIN, *Centrabl. f. d. med. Wiss.* 1866 ; *Arch.. ftd. ges. Physiol.*, 1868 ; Unters. und d. Erregungsvorgang in Nerven u. Muskeln. 1891.—DU BOIS-REYMOND, *Jahresb. d. phys. Ges. zu Berlin*, II, 1845.—CHAUVEAU, *C. R. Acad. sc.*, t. LXXXVII, 1878, pp. 95, 138, 238.—GRIGORESCU, *Biol.*, 1891 ; *Biol.*,

1892, p. 634 ; *Arch. physiol.*, 1894 ; Helmholtz, *Monatsb. d. Berl. Acad.*, 1850, 1854 ; *Arch. f. Anat. und Phys.*, 1850, 1852.—Helmholtz et Baxt (mesure chez l'homme), *Monatsb. d. Berl. Acad.*, 1867, 1870.—Hermann, *Handbuch*, 2 vol., 1 partie.—Marey, *Gaz. méd.*, Paris, 1866 ; Du mouvem. dans les fonctions de la vie, Paris, 1868.—H. Munk, *Arch. f. Anat. und Physiol.*, 1860.—Place, *Arch. v. Pflüger*, 1870, t. III, p. 424.—Regnard, Influence des hautes pressions, *Biol.*, 1887, p. 406.—Valentin, *Molesch. Unters.*, X, 1898.—Wundt, *Arch. f. d. ges. Physiol.*, 1870 ; Unters. z. Mechan. d. Nerv. und Musk., II, Stuttgart, 1876.

Rate ; sensory nerves.—Bloch, *Arch. d. physiol. sc. exp.*, 1875, p. 588.—Hirsch, *Molesch. Unters.*, IX, p. 183.—De Jaager, *Arch. f. Anat. und Phys.*, 1868, p. 657.—Kohlrausch, *Zeitsch. f. rat. Med.*, XXVIII, 1866, et XXXI, 1868.—Schelske, *Arch. f. Anat. und Phys.*, 1864, p. 151.—V. Wittich, *Zeitsch. f. rat. Med.*, XXXI, 1868, p. 87.

Electricity (Ouvrages généraux à consulter).—Bordier, Précis d'électrothérapie, Paris, J.-B. Baillière, et fils ; Précis de physique biologique (Collection Testut), Paris, O. Doin.—Broca, Art. "Electricité," *Diction. de physiol.* de Richet.—Joubert, Traité élémentaire d'électricité.—O. Lodge, Les théories modernes de l'électricité, traduit de l'anglais par Meylan, Paris, Gauthier-Villars et fils, 1891.—C. Maxwell, Traité élémentaire d'électricité, traduit de l'anglais par G. Richard, Paris, Gauthier-Villars, 1884.—Poincaré, La théorie de Maxwell et les oscillations hertziennes (Collection *Scientia*), Paris, G. Carré et C. Naud.

Excitability of nerves.—D'Arsonval, Durée après la mort, *C. R. Acad. sc.*, t. CXVI, 1893, p. 1530.—C. Bernard, Œuvres diverses, Leçons sur le syst. nerveux. —Brown-Séquard, *Arch. physiol.*, 1892.—Gotch, Infl. tempér., *Journ. of Phys.*, 1896, p. 247.—Howell, Budgett et Léonard, *Journ. of Physiol.*, 1894, p. 298.—Stefani, *Arch. ital. de biol.*, 1899, t. XXXII, p. 439.—Tissot, Persist. après la mort, *Arch. de physiol.*, 1894, p. 142.—Tschiriew, *Arch. f. Anat. und Phys.*, 1877, p. 489.—G. Weiss, Légère traction, *C. R. Acad. sc.*, 1899, t. CXXVIII, p. 452.—Zederbaum, Einfl. d. Dehnung, *Arch. f. Anat. und Phys.*, 1882, p. 116.

Excitability and conductivity.—Gad, *Arch. f. Anat. und Phys.*, 1887, p. 363 : 1888, p. 395, et 1889, p. 350.—Pistrowski, *Arch. f. Anat. und Phys.*, 1893, p. 205.

Excitation of nerves.—D'Arsonval, *C. R. Acad. sc.*, 1881, t. XCII, p. 1520 ; 1891, t. CXII, p. 625 ; *Arch. de physiol.*, 1889, p. 246, et 1893, p. 387.—Bernheim, *Arch. v. Pflüger*, 1874, t. VII, p. 60.—Bordier, *Arch. de physiol.*, 1897, p. 543.—Boudet (de Paris), *Trav. lab. Marey*.—Charbonnel-Salle, Thèse Fac. sc. Paris, 1881.—Dubois, *Arch. de physiol.*, 1897, p. 746.—Engelmann, Beweg. an Nervenfas. b. Reizung mit Induct. schl., *Arch. v. Pflüger*, 1872, t. V, p. 31.—Hallsten, *Arch. f. Anat. und Phys.* 1881, p. 90.—Hoorweg, *Arch. de physiol.* 1898, p. 269.—Kries, *Arch. f. Anat und Phys.* 1884, p. 337.—Lewandowsky, *Arch. f. Anat. und Phys.*, 1899, p. 352.—Marchand, Excit. des centres, *Arch. v. Pflüger*, 1878, t. XVII, p. 511.—Oelh, *Arch. ital. de biol.* 1891, 1893, 1898.—Sestchenow, *Arch. v. Pflüger*, 1872, t. V, p. 114.—Tiegel, *Arch. v. Pflüger*, 1876, t. XIII, p. 598.—Wedenski, *Arch. de physiol.*, 1891, p. 687.—G. Weiss, *C. R. Acad. sc.*, 1897 ; *Biol.* et *Congrès de physiol. de Turin*, 1901.

Interferences.—Charpentier, *C. R. Acad. sc.* et *Arch. de physiol.*—Patrizzi, *Arch. ital. de biol.*, 1896, t. XXV, p. 1.—Valentin, *Arch. v. Pflüger*, t. XIII, 1876, p. 320.—Wedensky, *C. R. Acad. sc.*, 1893, t. CXVII, p. 240.

Chemical excitants.—E.-W. Groves, *Journ. of Physiol.*, 1893, p. 221.—Stefani, *Arch. ital. de biol.*, 1895, t. XXII, p. 183.—Sven Akerlund, *Arch. f. Anat. und Phys.*, 1891, p. 279.—Wertheimer, *Arch. de physiol.*, 1890, p. 790.

Polar action ; unipolar excitation.—A. Charpentier, *C. R. Acad. sc.*, 1893 et 1899 ; *Arch. de physiol.*. 1893, à 1899.—Chauveau, Effets physiol. électric. *J. Anat. et Phys.*, de B.S., 1859 ; Utilisation de la tension électroscopique, *Soc. avanc. sc.*, Lyon, 1874 ; Excitation unipolaire, *C. R. Acad. sc.*, 1875-1876.—Courtade, *Arch. physiol.*, 1890, p. 579.—Engesser, *Arch. v. Pflüger*, 1875, t. X, p. 147.—Leduc, *C. R. Acad. sc.*, 1900, t. CXXX, p. 524 et 730.—Magini, *Arch. ital. de biol.*, 1883, t. IV, p. 278.—O. Nasse, *Arch. v. Pflüger*, 1870, t. III, p. 476.—H. Sewall, *Journ. of Physiol.*, 1880, 2, vol. III, p. 175.

Sinusoidal voltaisation.—D'Arsonval, *Arch. de physiol.*, 1893, p. 387.

Currents of high frequency.—D'Arsonval, *Arch. de physiol.*, 1893, p. 401.—Bordier et Lecomte, *C. R. Acad. sc.*, 1901.—Radzikowski, *Trav. lab. Instit. Solvay*, t. III, fasc. I.

Magnetic field ; waves, electric rays.—Danilewski, *Arch. de physiol.*, 1897.—Radzikowski, *Trav. lab. Instit. Solvay*, t. III, fasc. I.

Latent stimulation.—Bernstein, *Arch. f. Anat. und Phys.*, 1882, p. 329.—Boruttau, *Arch. f. Anat. und Phys.*, 1892, p. 454.—Johan. Gad, *Arch. f. Anat. und Phys.*, 1886, p. 263.—Mendelsohn, *Arch. de physiol.*, 1880, p. 193.

Local excitability of the different portions of the nerve.—A. Beck, *Arch. f. Anat. und Phys.*, 1897, p. 415, et 1898, p. 281.—Imm. Munk et P. Schultz, *Arch. f. Anat. und Phys.*, 1898, p. 297.

Repeated excitations : physiological tetanus.—CH. BOHR, *Arch. f. Anat. und Phys.*, 1882, p. 233.—CYON, Electrothérapie.—DUCHENNE, Electrisation localisée.—GRÜNHAGEN, *Arch. v. Pflüger*, 1872, t. VI, p. 157.—KOHNSTAMM, *Arch. f. Anat. und Phys.*, 1893, p. 125.—KRIES und SEWALL, *Arch. und Phys.*, 1881, p. 66.—KRONECKER und NICOLAÏDES, *Arch. f. Anat. und Phys.*, 1883, p. 27.—KRONECKER und STIRLING, *Arch. f. Anat. und Phys.*, 1878.—VON FREY, *Arch. f. Anat. und Phys.*, 1883, p. 43.—FRIED. MARTIUS, *Arch. f. Anat. und Phys.*, 1883, p. 542.—SCHOENLEIN, *Arch. f. Anat. und Phys.*, 1882, p. 357 et p. 369.—VALENTIN, *Arch. v. Pflüger*, 1875, t. XI, p. 481.

CHAPTER II

NERVE ENERGIES

THE study of the muscle serves as model for that of the nerve; but this latter study is incomparably less advanced, which is due to special conditions affecting experimentation on the nerve, these being less favourable than in the case of the muscle.

A. ENERGIES WHICH ARE DETECTABLE IN THE NERVE; ORIGIN AND SUCCESSION

In the muscle, energy in its initial condition is of chemical nature; in its final state, it appears as heat and as mechanical work; its intermediate transformations elude our observation; we know, however, that certain electro motor phenomena are connected with the production of this work. In the nerve, we must suppose that a cycle of the same nature exists; but, far from being able to indicate precisely the different conditions of the transformation of energy, we can merely vaguely point them out.

Initial condition.—In the nerve, the initial energy should also be chemical; as a proof of this may be cited the faculty which the nerve possesses (as does every tissue) of breathing, that is to say, of burning up something in taking up oxygen from the blood and in returning to the latter carbonic acid;—the final and the intermediate energies are far less accurately known; however, to the nerve must be ascribed electromotor phenomena analogous to those of the muscle.

Final condition.—Chauveau teaches that nervous energy should be capable of entire reappearance in the form of heat, almost as in the case of the muscle, which contracts *in vacuo*, when no mechanical work is produced. According to him, this heat, arising at the point of termination of the nerves within the muscle, is added to that of the muscle, and may even increase it to such a degree that it may be appreciable by the thermometer.

Yet this final state of all nervous energy is not that which occupies our attention when we desire to express the special impulse which the nerve brings to bear on the muscle (or any organ external to the latter) in order to overcome its molecular equilibrium and to cause it to expend its own individual energy. It is scarcely admissible that this shock is the result of calorific vibrations. Probably in this case, as in that of the majority of organs, heat merely follows or accompanies molecular work of a special nature which is accomplished by the motor nerve terminations in the muscle, in order to arouse in the latter an excitable condition.

It has been asked, without it being possible to give an answer, if this work is of an electrical nature. This idea has been suggested by the analogy which has been remarked between the nerve and certain electrical apparatus, and also by the fact that, amongst the artificial stimuli of the muscle and of the tissues, electricity is the best known. But these are rough analogies whose insufficiency is obvious. An opinion on this subject can only be based on direct and convincing experiment. Unfortunately, we have no means of isolating the nerve terminations in order to collect directly from them the energies which they give off, and to determine how these latter affect the apparatus ordinarily used in physics.

Transmitted and localized energies.—The initial and final conditions of energy in the nerve may be regarded in two different ways. They may, for example, point out as regards the first the form assumed by the energy at its entrance into the receptive pole of the neuron, and as concerns the second, that at its exit from the ramified extremities of the distributing pole : thus the process of nerve conduction is carried out. They may also express—and this is their most general sense—the successive forms of energy in each section, or at each point, of the isolated nerve.

Source of energy and excitation.—Whatever idea indeed may be formed of the process of conduction or of the circulation of energy in the direction of the length of the fibres, it is necessary to admit that, at each point of the nerve, a local circulation of energy exists from the interior to the exterior, for this is proved by the exchanges with the blood at the point of contact with the capillaries which accompany the nerve throughout its length. It may indeed be said that, just as in the case of the muscle, this is the source from which energy is supplied, and that the latter does not take its rise in the centres or in the organs of special sense. As in the case of the muscle also, the source, properly so called, of energy which lies in the vessels must be distinguished from the source of the stimulation which comes to it from other nerves or from the surrounding medium by the intermediation of differentiated peripheral organs. The difference between it and the muscle consists in the fact that, in the latter, the expenditure of energy being the end of function, this energy circulates in it in a relatively enormous quantity ; while in the nerve, conduction and excitation being the end of function, the current in it is infinitely weaker, whence the difficulty of estimating it, or even of proving its presence.

Reserve of energy.—Yet, further, as in the muscle, this energy is not abstracted from the blood by the nerve immediately, at each moment of its functional activity, but is stored up in its tissue, in the form of an alimentary intracellular reserve, which is expended (probably by combustion) in proportion to its activity. In this way it is possible to explain how it is that this activity may persist in the nerve for sometime after all its connexions in the vascular system have been destroyed, and how it is that this activity definitely ceases when this isolation has lasted for too long a time. Of the nature of the substance representing the stored-up energy nothing is known ; it may be, under its form of a mobile and immediately utilizable reserve, a hydrocarbon, as in the case of the muscle, and, in its dormant form, one of the fats which surround the axon.

Experiment teaches us further that the reserve of energy in the nerve, which is immediately available, forms but a small portion of its total reserve. Each single stimulation gives rise in the nerve (and by rebound in the muscle) to a very limited expenditure of its total potential energy. The reconstitution of the portion expended is effected so rapidly that it seems to be an opposite and necessary phase of this expenditure, so long as the provision is not exhausted. When the nerve is separated from its vessels, this exhaustion is fatal ; when the nerve maintains its vascular connexions this exhaustion is very difficult to obtain, whence arises the somewhat exaggerated but relatively true notion, that the nerve is *incapable of fatigue*.

This limitation in the expenditure agrees with another experimental fact, namely, that the activity of the nerve, like that of the muscle, can only be maintained by an incessant renewal of the excitation in it. Since Weber, every time that we see a muscle in a state of tonic, that is to say, continuous contraction, we regard it as receiving from its motor nerve successive closely approximated but discontinuous impulsions, while at the same time the nerve receives them in the same order from the apparatus which excites it. We know indeed that the only correct way of obtaining this prolonged tension of the muscle is to supply it with impulsions of this order, and the employment of the interrupter (*trembleur*) of du Bois-Reymond corresponds to this necessity.

To return to the energies which can be detected in the nerve. There are two which have been particularly studied and established in it : heat and electricity.

Heat developed by the nerve.—The amount of heat given off by the nerve tissue is extremely small. In isolated nerve trunks it eludes observation, as is shown by the experiments of Rolleston, Stewart and of Boeck, who have endeavoured to estimate it without result, using apparatus (bolometres) sensitive up to $\frac{1}{5000}$ of a degree. In the brain, Mosso, by producing asphyxia, has caused obvious heat production, which may be fairly attributed to a local process, but without producing the complication of displacement of heat brought from another part by the circulation (see *Animal Heat*, pages 389–396). Chauveau considers, for his part, that a small fraction of the heat evolved by muscle, during its stimulation, may be due to the nerve terminations. To this is limited our knowledge concerning the heat given off by the nervous system.

Electricity developed in the nerve has been the subject of a very large number of researches and observations, and hence merits a separate study.

B. ELECTRIC ENERGY OF NERVE

The nerve is the seat of *electromotive forces* which are fairly easy to investigate. But their study necessitates a mutilation of the organ examined, and thus much complicates the conditions of the experiment and the explanations which are given of it.

1. **Current of repose.**—As has been remarked above, no means exists by which the neurons can be isolated, in the sense of detaching them from their connexions at either extremity and of observing what passes at each of these extremities. We are compelled to experiment on fragments taken from the continuity of the nerves.

Experiment.—Let a segment of nerve isolated by two sections be taken ; this small nervous cylinder will be seen to present at its surface an altogether special distribution of the electrical potential. *Starting from the middle zone, which is*

known as its equator, this potential is observed to gradually fall, in proportion as the two extremities are approached. Between the equator and each of the extremities, this difference is at its maximum; between points which are more nearly approximated, it is less in proportion as the distance itself is less. Between the two extremities, as between all points symmetrically situated as regards the equator, it is *nil*.

If this segment of nerve be cut in two, each one of the two halves presents individually the same distribution of potential. The case is obviously analogous to that of a magnet which is broken in pieces, and of which each fragment is furnished with two poles, just as the primitive magnet of which it forms a portion; but with this difference, that the detached fragments of the nerve are not furnished with opposite poles at their extremities, but the two poles of the same nature are electrically opposed to their equator. So far as it is possible to carry this analysis, this arrangement and distribution of the potential will be found to be present and symmetrically repeated as concerns the two halves of all the fragments. A fragment of nerve fibre will be found to behave in the same manner. It is possible that the component particles of the fibre, inasmuch as these particles represent the elementary organization of the nervous protoplasm, would present the same phenomenon. The reasoning, indeed, is applicable both to the nerve and to the magnet; analysis in both cases proves that the distribution of the polarities is connected with the molecular structure, or with the component particles, these being of extreme tenuity.

Intensity.—When an attempt is made to estimate the intensity of the current of repose, that which is determined is the intensity of the derivation received in the galvanometer. The intensity of the derivation is about 0·02 Daniel (or about 0·02 volts). *It varies little between different animals, equally little between different nerves*, whether motor, sensory, or mixed; but it is stronger in the non-myelinated nerves than in those provided with myelin (Kuhne and Steiner). Frederic has ascertained it to be 0·048 (Daniel) in the lobster.

Origin of the electric currents of nerve.—To what must the currents which are thus observed in nerves be attributed? Are they the result of a merely local reaction of the metallic electrodes on the nervous tissue? No, because they are equally well, or even better observed when *inactive and non-polarizable* electrodes are made use of to collect them. The differences of potential which give rise to them must then pre-exist in the separated nerve segment, and this apart from any contact of the conductors by which they are carried to circulate in the galvanometer. The nerve segment, or rather, the particles which compose it, seem at the first glance to resemble open cells, in which the current only circulates when their polar wires are united.

Derived currents.—This hypothesis may be brought forward; but it may also be asserted, and with more probability, that these particles (like those of the magnet) are the seats of currents completed in themselves (much more complicated, it is true, than those of the magnet). When the nerve segment is connected with the galvanometer by two points on its surface which are unsymmetrically situated, there arises merely a derivation of these particular currents, similar to that which occurs in a battery circuit when two of the points of its interpolar wire are united by a second closed wire which passes through a galvanometer.

Do nerve currents pre-exist?—We have just seen that they pre-exist as regards the application of electrodes, but do they exist anterior to the mutilation of the nerve which is affected in order that the segment to be examined may be removed? In other words, will an isolated neuron, not broken by the cutting instrument, present them? This question is still under discussion; nevertheless, many physiologists think, with Hermann, that the answer is in the negative. Du Bois-Reymond regarded the currents thus observed in the nerve, apart from any func-

tional activity, as being *currents of repose* ; Hermann describes them as *currents of alteration.*

Current of alteration.—Section of the nerve trunk by the cutting instrument does not merely separate the component particles of the fibres of this nerve ; it necessarily destroys the structure of these fibres to a certain extent, mixes the separated substances, which hence react amongst themselves, without taking account of the fact that the air penetrates and probably takes part in these reactions. Hence the origin of currents of chemical source, but which arise under entirely artificial conditions. They would not have much interest for us if they were not themselves the image of converse currents, more feeble, indeed, but otherwise altogether similar, which are connected with the functional activity of the nerve at the instant of stimulation. But these last are not observed without the complication arising from the presence of the first.

Transverse longitudinal current ; axial current.—In the case of a detached segment of nerve, the greatest difference of potential is observed between its equator and one or other of its cut extremities. This is obvious when the equator, as also one of the two extremities (by non-polarizable electrodes) is connected with the galvanometer. But between the two extremities the potential value is not equal ; if, indeed, the two ends of the nerve segment are connected with the galvanometer, the existence of a much feebler current, which Mendelssohn has observed, and called the *axial current*, becomes obvious in opposition to the preceding current, which is the *transverse longitudinal* current ; *its intensity is about ten times less* than that of this latter. The interest of the axial current arises from the fact that it has a definite orientation with regard to the physiological conduction of the nerve under examination. *As regards this latter conduction, it has an opposite direction* ; it is ascending in the posterior roots (centripetal) and descending in the anterior roots (centrifugal). Is this orientation of the axial current connected with the mechanism of the phenomena of conduction, or rather is it allied to a phenomenon of a trophic nature, of alteration, which would be unequal in the two ends, according to the respective locality they occupy in the intact nerve with regard to the cell ? This is not precisely known. Like the transverse longitudinal current, the axial current undergoes a modification of its intensity (negative variation) through the fact of the activity of the nerve, when the latter is stimulated.

2. **Negative variation : current of action.**—Let a nerve segment be prepared in such a way that two unsymmetrical points are connected

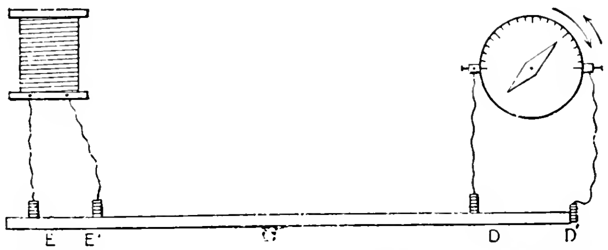


FIG. 37.—Diagram of an experiment for the determination and estimation of the negative variation.

EE′, DD′, living nerve. In EE′ excitation. In DD′ derivation of the longitudino-transverse current, called that of repose or alteration, whose direction is indicated by the largest of the two arrows. At the moment of excitation, contrary current of less intensity which declares itself as a negative variation of the longitudino-transverse current.

with the terminals of the galvanometer. The needle of the latter deviates in a certain direction to a certain extent which is recorded. The other extremity of this nerve is stimulated; the needle returns towards zero, but without attaining this point, thus indicating either a diminution of the intensity of the so-called current of repose, giving rise to what is known as the *negative variation* (du Bois-Reymond); or an inverse current of less intensity than the current of alteration, and which, on this hypothesis, is known as the *current of action*.

Its importance.—Whatever explanation may be given of it, this phenomenon is a very important one, because it is obviously allied to the active condition of nerves; this may be inferred from the following observations:—

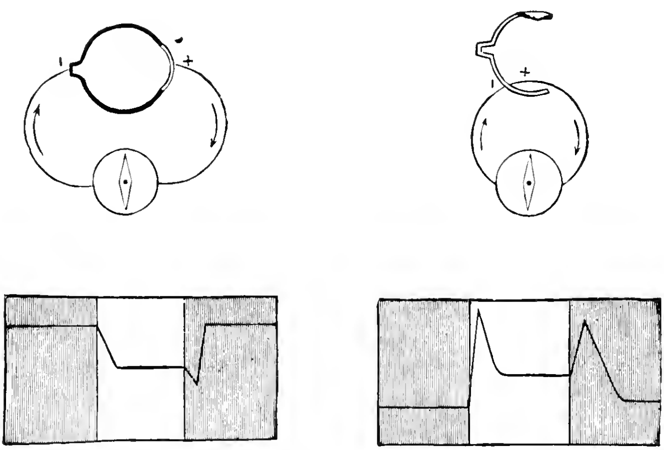


FIG. 38.—Currents of the optic nerve and of the retina.

Above, diagram of the arrangement of the experiment. Below, graphic expression of the modifications of these currents during repose (darkness) and activity (illumination).

The darkness is marked by hatching.

On the left, *current of alteration of the optic nerve*. The surface of section is negative with regard to the longitudinal surface. During illumination, this negative condition is diminished. When the illumination ceases it also diminishes slightly; then the current returns to its initial value (Kuhne and Steiner).

On the right, *retinal current*. The surface of the rods is negative with regard to that of the fibres. During illumination, this negative condition is at first increased, it then becomes less marked (sometimes diminished). On the interruption of the illumination, fresh augmentation; then return to the initial condition (Kuhner and Steiner).

(a) *The magnitude of the negative variation is definitely related to that of the stimulation*, just as is the magnitude of the muscular contraction. A. Waller has verified this point as concerns segments of detached nerves experimented upon in the moist chamber. He has noticed, it is true, that, when the intensity of the stimulation exceeds that which, in the case of a nerve *in situ*, would give rise to maximum contractions, the magnitude of the negative variation is still capable

of increase. The negative variation being the special response of the nerve to stimulation, and contraction that of the muscle to stimulation transmitted by the nerve, there is no reason why the limits of sensation should be the same in the two organs. But the parallel progression of the two reactions demonstrates their union in nervo-muscular function.

(b) *Its time of propagation* (interval of time which separates it from the stimulation) *is definitely connected with the length of the course which it runs,* and it is the same as for the muscular contraction. We may thus substitute the negative variation for the muscular contraction as evidence of nervous activity. As regards the superficial or deep nerves, which have no direct connexion with the muscles, it may serve as a means of research and of control in the study of their special functions.

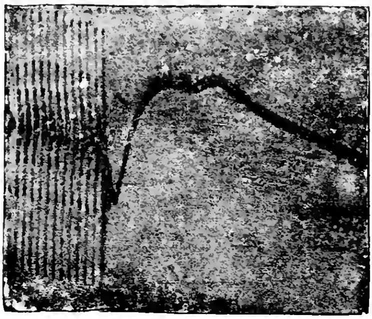


FIG. 39.—Action of anæsthetics (chloroform) on the internal activity of the nerve (negative variation), after Waller.

On the left, series of negative variations obtained by stimulating the nerve not submitted to anæsthetic vapours. On the right, absence of the negative variations during anæsthesia. The current of repose at this moment presents slow variations in its intensity.

(c) *The negative variation is independent of the nature of the excitation made use of.* It may be elicited by stimuli other than electricity, and more especially by the physiological excitant, in other words, the normal excitant of the nerve itself. Holmgren, Kuhne and Steiner have demonstrated it in the optic nerve and in the retina, by subjecting the latter to its specific excitant—light. Beauregard and Dupuy have observed it in the acoustic nerve, by stimulating the internal ear by the sonorous waves. Du Bois-Reymond had already noticed that it may be elicited in the motor nerve, by stimulating the latter in a reflex manner by means of a sensory nerve. It may also be elicited by the excitation of the cerebral motor area.

(d) *The negative variation is no longer produced when the nerve is subjected to the action of anæsthetics* (Waller). In every way, then, it is closely connected with the activity of the nerve, and may be taken as evidence and measure of this activity.

Wave of excitation or of propagation of excitation.—From what has just been said, it may be inferred that *the negative variation is connected, in each section of the nerve, with the excitation of this section during the passage of the latter.* In other words, it is connected with what is commonly called *the wave of excitation ;* assuredly a very complex phenomenon, in which, as has been seen, electricity takes a part, but which we have no right, nor even any plausible reason,

to call an electric wave, that is to say, one similar to those which pass through the wires of the telegraph, or which are transmitted through dielectrics.

If, following the example of the majority, we neglect the current of alteration, which is wanting in normal conditions, we shall represent the negative variation as *a wave of negative potential* (abbreviated into *negative wave*), which passes through the nerve from one extremity to the other. As a potential of a given denomination cannot exist apart from a potential of the opposite denomination, it follows that, at its entry into the nerve, it is confined to a positive zone, which is in front of it ; at its exit to a positive zone which is behind it ; in its course it is comprised between two positive zones, the one in front, the other behind it.

Diphasic current.—In passing from the commencement to the end of the nerve, the relationship of the negative and positive zone is inverted. What is known as the current of action acts in the same way. Let a nerve trunk be prepared whose two ends are connected with the galvanometer ; if an impulse passes through it from one end to the other, the galvanometer (if sufficiently mobile) will undergo two oscillations, the one opposed to the other, corresponding to the entrance and exit of the impulse.

The diphasic variation of the currents is difficult to demonstrate in nerves, but is easily observed in the case of muscles, especially the heart, which presents a real and somewhat slow wave of propagation of the impulse through its fibres. The electric currents of nerve and of muscle are sufficiently similar to be expressed under the same general formula.

Form of the lines of flow of the current of action in the stimulated point.—Considered in a given section of the continuity of the nerve (in the middle of its length, for example), the negative variation, save that its differences of potential are weaker and its polarities inverted, recalls the distribution of the so-called current of repose or of alteration of the nerve ; it is capable of being depicted in a similar manner. In this case the equator is of a higher potential than the extremities. As to the current of repose, it may be asked if these potentials correspond to opposed non-satisfied tensions, or rather to true currents circulating in completed circuits.

The latter supposition is probably correct. These circuits may be depicted as follows : on the surface of the stimulated nerve (or that of the nerve molecules), their lines of flux proceed to meet each other, but without actually doing so, in a direction parallel to the length of the nerve ; having arrived at the negative zone, they return, follow the opposite direction in the depth of the nerve and complete the circuit. In this way these currents form a double series of rings arranged round a common axis. They may be compared to two tyres fixed on the same axis, in which the currents circulate in opposite directions. It will be noticed that in such a tyre *the lines of force circulate only in the interior.*

Displacement of the phenomenon with the propagation of the impulse.—In proportion as the wave progresses in the nerve, the potential is inverted in the sections which follow each other. Each section, taken by itself, is indeed positive when the impulse approaches it, negative when the latter reaches it, once again positive when it leaves it.

We know the rate of the progression of this wave, but we are ignorant of its length ; in acting in the manner just mentioned, we do not employ, indeed, any direct or indirect means which are really accurate in order to appreciate it. We shall demonstrate, a little farther on, a method different from the preceding, which has been contrived for the purpose of measuring it.

If the nerve is invaded by a series of successive impulses very closely approximated (such as induction shocks), it will evidently be traversed by a series of these waves which, arriving one by one at its extremity, will give rise in it to a series of variations of the current of the same rhythm as themselves. If these variable currents are received in a telephone they will produce a sound whose

pitch indicates their number in a given time. If they are received by a galvanometer, the needle, owing to its inertia, will not return to its initial condition during the very short intervals between these successive variations, and will maintain a median position so long as these impulses last.

Intensity of the current of action, or of the negative variation.—As for the current of repose, this word *intensity* must be understood in a purely *relative* sense, because the absolute value of the phenomenon is unknown. And for this reason. The wires of the galvanometer being arranged on a section of nerve in an appropriate manner, at the instant when currents arise in this segment they are divided into two portions ; the one (principal current) circulates in the nerve, the other (derived current) circulates in the galvanometer. In this case there is no means of ascertaining the connexion, as regards magnitude, which exists between the principal and the derived current. It is only known that *the direction of the derived current is the same as that of the principal current, and that its intensity is proportional to it ;* yet this is very valuable information. It is possible that the derived current is but a very small fraction of the internal current of the nerve, and that it represents merely the losses of the latter, which are due to faulty isolation, losses which are, however, too minute to alter the functional activity of the nerve. It is remarkable that, in case of a nerve *in situ* and unmutilated, only a very weak derivation is manifested when it is treated in the manner which has just been referred to ; to observe the negative variation a cut nerve must be operated on, just as if the section had the effect of opening up some of the closed cycles in which the currents circulate.

(a) *Intensity in relation to the current of repose or of alteration.*—Measured, as has just been observed, by the derived current which is received in the galvanometer, *the intensity of the negative variation is much feebler than that of the so-called current of repose or of alteration.*—It represents in the frog about the tenth part of it, and still less in mammals. Its denomination of negative variation takes its origin from the fact that it always presents itself as a diminution of this current of repose. Whether, indeed, the current of repose really pre-exists, or whether it arises through the mutilation of the nerve, which is necessary in order that the internal circuits of nerve elements may be made manifest by our galvanometers, the electrical phenomenon which is connected with the activity of the nerve during its stimulation only appears to us as a converse (but unequal) modification of this current which we cannot avoid under the ordinary experimental conditions. Other things being equal, the negative variation will be the greater in proportion as the current of repose is greater. When there is no current of repose, there is no negative variation.

(b) *Intensity in relation to the magnitude of the excitation.*—As has been said above, the intensity of the negative variation is definitely related to the intensity of the excitation. It increases with the latter up to a maximum which is not exceeded. It behaves itself in this regard like muscular contraction ; it has nearly the same threshold as the latter ; and closely follows its variations.

Remark.—The excitations which are brought to bear on a nerve are either *simple* (isolated closing or opening of the circuit, induction shock, static discharge), or *composite* (due to the repetition of a certain number of stimuli in a given interval of time). In order to observe negative variation, composite excitations are habitually employed (called tetanizing). The reason of this is that in order to overcome the inertia of the needle of the galvanometer, or that of the mercurial column of a capillary electrometer, it is necessary that the impulses which arise from the electric current be repeated a certain number of times. These successive impulses fix the needle in the median position, or that of relative immobility. The form of movement of a galvanometric needle does not in this case reproduce the elementary form of the electrical phenomena under obser-

vation, nor its periods; it merely shows the general tenour of it. When the experiment is conducted, no longer on myelinated nerves, but upon non-myelinated nerves, in which the current of repose is stronger and the negative variation greater, the simple excitations produced by induction shocks, or even the breaking or making of a constant current, become competent to produce a corresponding isolated negative variation. In these conditions, and thanks to certain contrivances, into the details of which we cannot enter here, it is possible to closely follow the general form of the electrical modification thus produced.

Form of the negative variation.—This form closely resembles that of a muscular contraction. Its period of augmentation is abrupt and immediately followed by a period of decline which is much longer.

Positive variation.—When the negative variation is over, it is followed by an inverse variation of positive direction, which is more or less marked, and which may be absent. In the case of a nerve which has been mutilated in order to produce the derivation proceeding to the galvanometer, before any stimulation there may be observed: (1) a so-called current of repose; (2) at the moment of stimulation a negative variation of this current of repose; (3) a positive variation of this current of repose. Some authors think, with Hering, that the positive variation is connected with the phenomena of nerve restoration after stimulation, just as the negative variation is connected with the waste of this nerve during its excitation.

Unipolar methods for the study of electrical variations of the nerve.—In the preceding experiments the excitations supplied to the nerve are bipolar, and the electrical phenomenon which is the consequence of them is a modification of its current of action received in a derived circuit which passes through the galvanometer. In other words, the nerve, in two localities separated the one from the other, is intercalated in two circuits, the one intended to provide the current which excites it, the other intended to receive the current arising in it as the result of excitation. But the nerve may be also stimulated in a unipolar fashion, in a single point of its progress; and, on the other hand, if the nerve presents at a distance a variation of its potential, it is possible, by connecting it to the earth by a conductor which passes through a galvanometer, an electrometer, or a galvanoscopic paw, to act in a unipolar manner on these different rheoscopes, which will demonstrate, each one in its special way, the current which passes through them; the two first will undergo a deviation which will be of a different tenour according to the direction of the current (negative or positive), the last will respond by a muscular contraction. Precautions should be taken to prevent the stimulating current directly reaching the rheoscope, which is intended to demonstrate the current which takes origin in the stimulated nerve. By this means, therefore, it is possible to render evident the current of action of the nerve without mutilation of this latter, and without giving rise in advance to a current of alteration. This is maintained by Charpentier, who has contrived this method.

Oscillatory variations of the electric potential of the nerve during its stimulation.—According to this author, the nerve thus stimulated is traversed, from its point of excitation, by a wave which has obviously the same rate of propagation as the negative variation. This wave is accompanied with a variation of the potential and, on its passage to the point at which the nerve is connected with the rheoscope, this variation is made perceptible by the latter. On account of its very slow rate of progress, this wave is not that indeed of the stimulating current, but a physiological wave, in which electrical phenomena, amongst many others, take part. It should be noted that the stimulation which gives rise to it is not necessarily tetanizing, but may consist of a simple excitation, such as that which arises in the nerve from making or breaking the current. So far the phenomenon does not differ from that with which we are already acquainted,

except as regards the means employed to render it evident. The new fact brought forward by Charpentier consists in the *oscillatory nature of the variation of potential* which takes origin at the point stimulated, and is thence transmitted along the nerve. A simple stimulation (induction shock, making of current) produces, according to this author, not a half-oscillation like that which is known as negative variation, or even an entire oscillation, but a series of oscillations, which decrease locally while they are transmitted to a distance. To demonstrate the oscillatory nature of the phenomena, the possibility of making the communication of the conductor with the electrometer is limited to determinate and successively variable periods after the excitation of the nerve. It is then seen that the deviation of the instrument ensues, according to the length of these periods, in one or other direction, a certain number of times. Of these different periods which elapse between the moment of stimulation and that in which the deviation commences to manifest itself, the shorter serves to determine the rate of propagation according to the formula $V = \frac{e}{t}$.

A rate of propagation of 26^{m} 43 per second is found, that is to say, practically that which Bernstein has pointed out as being the rate of propagation of the negative variation in the nerves of the frog.

In comparing these different periods one with another we see that a

$\frac{1}{670}$ to $\frac{1}{800}$ of a second $= 0^{sec}$ 00134 $= t$.

After the formula $V\,t = \lambda$ (length of wave)

$$26{\cdot}43 \times \frac{1}{7475} = 0^{m}\ 035\ ;\ \text{whence}\ \tfrac{1}{2}\,\lambda = 17^{millim}\ 5.$$

The length of a wave $= 3^{cent}\ \frac{1}{2}$.

The frequency or number of oscillations per second = 750 circa.

Nature of the phenomenon.—It may be asked if this oscillatory phenomenon represents the negative variation (current of action), or an electrotonic modification of the nerve (polarization at a distance), both being thus proved to be less simple than has hitherto been supposed. The author of these researches maintains that it is not an electrotonic phenomenon, but a negative variation.

Nervous interferences.—Inasmuch as the nerve is, throughout its length, the seat of a series of waves which pass along it, and inasmuch as we are able to cause these waves to act on a rheoscope, it will be possible for us to make them act on it in such a manner that they interfere with one another in definite fashion. In order to accomplish this, two points of a nerve are chosen separated from one another by a wave length or half a wave length, and these two points are connected to the same electrometer or to the same galvanoscopic paw. In the first case (a wave length) the phases will be concordant; they will supplement one another in order to produce an electromotor effect, there will be a stronger deviation of the instrument or a stronger contraction of the frog's foot; in the second case (half a wave length) the phases will be discordant and opposed, they will neutralize each other; there will be immobility of the instrument and repose of the frog's foot.

Electrical resistance of the nerve. — Compared to a rod of copper having the same form and dimensions, a nerve is a very inferior conductor. The numerical estimations which have been made of its resistance have no great value, because its electrically active substance may be extremely reduced with regard to the protective or nourishing materials which enter into the composition both of the nerve and of its constituent elements. It is as if a tube of copper were compared to a similar tube of paraffin containing extremely fine copper wires in its interior. The most interesting observation is the determination of the variations of this resistance as regards their connexion with the activity of the nerve. Charpentier has found that *the electrical resistance of the nerve increases with its activity; and that, on the contrary, it diminishes when its physiological properties disappear.*

Cocaine diminishes it, curare and strychnine at first diminish it for sometime, but afterwards increase it; crushing of the nerve causes it to fall by a half. This increase in resistance of the nerve during activity is attributable, according to this author, to the development of an opposing electromotive force which represents the physiological work (the expenditure of energy of the nerve) and serves to estimate it; he has found in one experiment that this expenditure is equal to $\frac{1}{200000000}$ of a kilogrammetre.

No lateral influence.—The electric currents whose intensity is capable of changing so abruptly are, in consequence of this faculty, liable to induce currents in circuits in their neighbourhood, if special precautions are not taken to avoid this influence at a distance.

Can the currents of action of one fibre excite, by influence, currents in a neighbouring fibre? Experience replies in the negative, and the least reflection shows that this must be so, otherwise nerves would discharge various and independent functions and would never act except simultaneously.

Part played by the cell in the transmission of excitation.—The impulse, in travelling from the receptive to the distributive pole of the neuron, passes through the body of the cell. Does it undergo some modification in it? This has been maintained, and the majority of neurologists still maintain it as a matter about which no discussion is allowable. I consider that experiment and reasoning both support the opposite thesis.

(a) *Arguments drawn from analogy.*—In the muscular element, it is not the granular protoplasm surrounding the nucleus which represents the contractile function, but rather its external, differentiated, striated portion: in the neuron, the differentiated function, strictly called nervous, is not that which surrounds the nucleus, but rather consists in the fibres to which this mass gives origin, and which pass through it in order to proceed to a greater or less distance.

(b) *Arguments drawn from experiment.*—There are neurons, such as those of the posterior root, which may be excited at will, either above or below their cell body; it is impossible to observe any real and constant difference in the effects of these stimulations; the cell produces no change in them, neither in the intensity, nor the latent period, and neither the form nor the distribution of the impulses is altered by it. Changes of this order, on the other hand, become marked when the impulse passes from one neuron to another in the felt works of the grey medullary matter. The experiment has been made on the frog (Morat).

Bethe has performed a still more convincing experiment. Taking advantage of the fact that, in certain animals, as the crab, these cells are attached to fibres by long pedicles arranged parallel to each other and perpendicularly to the fibres, he cuts these pedicles, and thus at the same time separates the cells, while preserving the continuity of the fibres throughout their length. The transmission of the impulses and the reflex movements to which they give rise remain possible for several days. Functional activity ceases at the end of this period, on account of the degeneration which the nerves, isolated from their trophic cells, undergo. This experiment proves both the independence of the fibres with regard to the cells so far as concerns the external or nervous function of these fibres, and their dependence so far as concerns the maintenance of their nutrition.

Exner (previously to the preceding authors) had studied, by the galvanometric method, the influence of the cells of the spinal ganglia on the transmission of impulses by the posterior roots. These roots, cut very close to the spinal

cord, are connected by their end, thus divided, to a galvanometer; a stimulus is applied to the nerve below the ganglion; the transmission of the impulse is effected through the ganglion just as through an ordinary nerve, there being no exaggeration of the latent period.

Contradictory experiments.—On the other hand, Gad and Joseph, experimenting on the jugular ganglion of the vagus, regarded as a spinal ganglion, and taking the respiratory movements as evidence of the reaction, have found that there is a difference in the duration of the period of latency when the excitations are made below or above the ganglion. According to these authors, the delay in the first case is from 0·123 of a second, in the second from 0·087; the difference of 0·036 between the two indicates the delay undergone by the impulses in their transit through the ganglion.

The structure of these ganglia, in reality less simple than was at first believed, will perhaps serve to explain these divergencies.

The following experiment has also been performed. Let an isolated segment of the spinal cord be prepared, and let all the sensory and motor nerves be cut, with the exception of one of these latter. This root is stimulated between the cord and the muscles which it supplies. The muscular contraction is registered. Then this root is cut close to the spinal cord; the stimulus is again applied and once again the muscular contraction is registered. According to Cyon, the first of the two contractions is longer than the second; this he attributes to a reflexion of the impulse which, starting from the point of stimulation, reascends towards the cord, redescends the same and arrives at the muscle immediately after the direct wave, in such a manner as markedly to lengthen it. Now I have repeated this experiment very carefully, but I have never found any appreciable difference between the contractions in the two conditions.

Modifications of the body of the cell during repose and functional activity.—The functional activity and the nutrition of the organs of cells are two things which may in principle be distinguished. One is often observed to be exaggerated, while the other is diminished, and conversely; but their limits are not clearly defined and, fundamentally, they are reciprocally connected. Activity of nerve elements is manifested, not merely by changes external to themselves (motion and sensation), but also by visible modifications of the protoplasm of the nerve cell. These modifications, consisting in change of volume of the cell, displacement of the nucleus, re-arrangement of the chromatic substance, have been studied by a large number of authors on different objects, such as the grey matter of the bulb, the ganglia of the great sympathetic, the retina, etc. The conclusions are slightly different, and sometimes contradictory the one to the other. Lugaro, who has undertaken critical investigation of the question, maintains that the cell increases in size when subjected to moderate excitation (electrical), while it again diminishes if the excitation is excessive. Speaking generally, an organ, when it becomes active, tends at the same time to increase its nutritive reserves by a compensatory exaggeration of assimilation over dis-assimilation; but, should the work be excessive, the compensation is insufficient and the reserves tend to become exhausted.

Chromatolysis.—Between the meshes of its network the cytoplasm of the nerve cell contains a substance which is stained by methylene blue (chromatine of Nissl). This substance is regarded by histologists as being a reserve for the neuron and is seen to disappear, starting from the nucleus, in the cells of the nerves which have been fatigued by stimulation (Vas, Mann, Lambert, Lugaro).

To the phenomenon of the disappearance of this substance the name

chromatolysis has been given ; it proceeds *pari passu* with the changes of volume of the cell and the mechanical displacements of the nucleus.

C. EFFECTS CONSECUTIVE TO STIMULATION : FATIGUE

Definition.—The word *fatigue* is used in two very different senses in ordinary language and in that of physiology respectively. In the first, it expresses a *sensation* which is united to the work of the bodily organs when this work tends to become excessive, and which warns us that repose is necessary ; in the second, it expresses not merely a sensation, but the *objective phenomena* of exhaustion and of the wear and tear of these organs, which checks their movement.

Thus the excess of activity tends to be self-limited ; but this is effected in two ways : the one, the most perfect, in which the regulation is carried out by a complex sequence, the nervous system intervening, and in which we once more observe the mutual relationship of motion and sensation ; the other, more elementary, in which work ceases through the absence of materials and of the conditions by which it can be supported.

In order to study the details of this objective phenomenon of exhaustion, the physiologist excites it himself in the different organs, including the nerves, by putting them in a condition which involves prolonged work. But, the activity of the nerve being estimated by that of the organ to which it communicates the impulse, it is necessary to have recourse to certain special contrivances in order to estimate its individual fatigue in that of the total of which it forms a part.

Resistance of nerves to fatigue.—When the stimulation of a nerve (a motor nerve for example) is prolonged beyond a certain limit, which varies according to circumstances, the contractions decrease and finally disappear. This result is attributed to the fatigue arising from the wear and tear, to the exhaustion of the excitable substance. At first it was supposed that this fatigue was equal in the nerve and in the muscle. Bernstein has proved that fatigue is far more marked as regards the muscle than as concerns the nerve.

How can this be explained ? All the methods employed may be reduced to the following : the transmission of the impulses between nerve and muscle is interrupted for a certain period ; the work of the first is increased vigorously and for a long time (in other words, forced fatigue is induced), while the second remains in repose ; then the connexion of the nerve with the muscle is re-established (or is allowed to re-establish itself), finally it is observed if the impulses of the first are transmitted to the second. If this is so, it is because it has resisted the fatigue which the long and strong stimulation to which it has been submitted has not failed to produce in the muscle.

Temporary dissociation of the muscular and nervous tissues. — What means are there for effecting this interruption, which should be only temporary? There are two: the action of the continuous current, and that of certain special poisons. Bernstein, and after him Wedinski, have brought about the temporary interruption by exciting a state of electrotonus in the nerve at its entrance into the muscle for a determinate time. Bowditch made use of curare, which is deemed to act only on the terminations of motor nerves, and Lambert has employed atropine, which acts in the same way on the nerves of the glands, in experiments carried out on secretory nerves. The removal of the obstacle takes place by the gradual and spontaneous elimination of the poison. If the stimulation of the nerve is maintained throughout the duration of the poisoning by curare or atropine, it is surprising to see, when this poisoning ceases, that the muscle contracts and the gland secretes, thus proving the transmission of the impulse, and therefore the absence of fatigue, in this nerve which has been kept so long in activity. But does poisoning by curare or atropine, as also the action of the constant current, respond to a simple interruption between the nerves and the organs which manifest changes in them, or has the nervous element become the seat of inertia throughout its length; in which case it would be no longer susceptible of stimulation and fatigue? Herzan prefers this second explanation, which he supports by experiments made on animals convulsed by strychnine; indeed, in these animals the nerve appears as inexcitable, and consequently as fatigued, as the muscle itself.

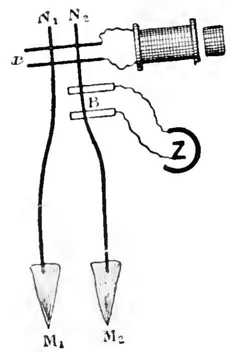


FIG. 40.—Indefatigableness of the nerves.

Two muscles, M_1, M_2, furnished with their nerves N_1, N_2, are simultaneously stimulated at x, by an induced current. The nerve N_2 is anelectrotonized at B by a constant current Z, so as to prevent the impulse reaching the muscle M_2, thus to prevent this muscle being fatigued. The muscle M_1 is quickly fatigued and ceases to contract. If then the cell current be broken, while the stimulation of the two nerves continues at x, the muscle M_2 will be seen to contract: therefore its nerve has not felt the effects of fatigue.

Wedinski, in order to eliminate these errors, investigates the activity of the nerve in a direct manner, by its negative variation, estimated by the aid of the galvanometer or the telephone: he finds that this variation exists so long as does stimulation itself, proving thus once again the *indefatigability*, which is at least relative, of the nerve.

Another method.—In the preceding experiments it is assumed that the agent (curare, atropine, electrotonization, etc.) made use of in order to physiologically separate the nerve from the muscle, localizes its action upon a definite and restricted area of the first (for example, curare on the motor plate) exclusively, and that the rest of the nerve preserves its normal activity, although hindered from manifesting it on account of its separation from the muscle. But it is possible that this hypothesis is inaccurate. Claude Bernard maintained that curare acts electively on the whole motor nerve; electrotonus is undoubtedly transmitted to a certain distance; and we do not know if the interior activity of a nerve, separated from its muscle, is precisely the same as that of a nerve which has preserved its natural connexions with it.

For all these reasons, Carvallo has had recourse to a method different to the preceding, by which fatigue of the muscle and of the nerve may be separately made evident. Two muscles of like nature and supplied with their nerves are kept exactly at the same fixed temperature. During this time one of the nerves

is subjected to temperatures varying from 0° to 30°, while all that happens from 10° to 10° is carefully noticed : it is ascertained *that there is a temperature most favourable for the motor nerve of the frog, which is* 20°. Above and below this temperature the susceptibility of the nerve decreases. The chilled nerve becomes fatigued more rapidly than the nerve at 20°. In a repeated series of excitations, it is noticed that the decrease of the contractions (the curve of fatigue) is brought about so much the more quickly as the temperature is lower. But the nerve at 0° and fatigued by stimulation recovers without delay its first excitability when the temperature once again becomes favourable to it ; that is to say, when stimulated, the temperature produces in the muscle work equal to that which this organ produced before. This result clearly shows that, although during the time that it was chilled, *the nerve was fatigued independently of the muscle,* and merely from the fact of the conditions of temperature in which it was placed ; the muscle, kept during this time at the same temperature, had no reason to undergo the effects of fatigue. Hence, in these conditions, and according to the conclusions of the author, fatigue would appertain to nerves, but not to muscles.

These experiments have also shown that, when a nerve is chilled to 0° over a certain limited portion of its course, and is fatigued by successive excitations, the portion thus chilled and fatigued (locally inexcitable) nevertheless conducts the impulse just as the non-chilled and non-fatigued portions. This fact supports the view of the non-identity of the two processes of excitation and conduction.

Conclusion.—From the fact that heat has a similar influence on the excitability of nerve, it must be concluded that this phenomenon of excitability (if not that of conductivity) is fundamentally of a chemical and not of a purely physical nature, in spite of the small quantity of energy which is made use of in producing it. The indefatigability of the nerves is only a smaller degree of fatigability in comparison with the muscles.

The mechanism of neuro-muscular fatigue.—Muscular or nervous fatigue is usually attributed to the exhaustion of cellular elements which have been functionally active for too long a time. Abelous remarks that this fatigue arises partly from the *products of disintegration* formed by this very activity, which act as paralysing or strictly speaking, "*curarizing*" substances on the nerve element. These waste products formed by muscle act on the motor nerve terminations by a kind of *auto-curarization.* When the nerve is subjected to the action of a tetanizing current, a moment arrives in which the contractions cease to occur ; but if then the muscle be directly stimulated, the latter is observed to respond to the stimulus ; this is practically the same result as is obtained with curare, except that the paralysing substance is in this case elaborated locally as the result of the muscular "*chimisme*" during contraction. Fatigue rapidly occurs in the case of individuals or animals whose suprarenal capsules are diseased (Addison's disease) or removed. It would thus be a function of these organs to neutralize the curarizing or paralysing action of muscular waste products. (Abelous, Charrin and Langlois.) See also Albanese, *Arch. of Biology,* 1892.

D. ELECTROTONUS.

The term *electrotonus* is applied to two orders of phenomena, the one physical (polarization), the other physiological (modifications of excitability), which take origin in this nerve when it is traversed by a current. For some (du Bois-Reymond, Pflüger), there would be a close connexion between the two orders of phenomena ; for others (Matteucci, Hermann), they would be entirely independent. Whatever the facts may be concerning this possible relation, the term *elec-*

trotonic condition should be reserved for the physical modification, and that of *electrotonus* for the physiological modification of the nerve; nevertheless, the two expressions are made use of indifferently in order to indicate, either the physical modification, or the physiological modification which arises from the passage of the current.

1. Electrotonic Condition.—Let a piece of nerve of a certain length be taken; it is placed on the two non-polarizable electrodes of a constant current, in such a manner that it extends beyond them on both sides, away from the portion submitted to the action of the current. Three areas may be defined in this piece of nerve: one *intrapolar* and two *extrapolar*.

If the portion of nerve arranged in this manner were an ordinary conductor (or if, through crushing, it had lost its nervous structure), the current would circulate only in the intrapolar portion. If it were a nerve in which both its structure and its vitality are preserved, in addition to the current which circulates in the intrapolar portion, electromotive forces will be developed in the extrapolar portions which will give rise in them to differences of potential between different points of its length, in such a way that, if two of these points be connected with the galvanometer, the existence of a current will be demonstrated.

Historical.—Longet and Guerard were the first who observed that, when a certain length of nerve is subjected to the action of the current of a battery, a current is developed (which they call *derived*) in the extrapolar region of the nerve (Longet, *Anat. and Physiol. of the Nervous System of Man*, t. I, 1842, p. 143). Matteucci, Gruenhagen, Hermann have endeavoured to establish the theory of these derivations, which they essentially attribute to the existence of a difference of electrical conductivity between the superposed layers of the nerve or of the nervous element. Du Bois-Reymond has studied the phenomenon in a detailed manner. He endeavours to explain it by his molecular theory (generally abandoned at the present time). Pflüger, Chauveau and many others after them have studied the modifications of excitability of the nerve which accompany electrotonic currents.

The terminology. — The battery current (or any other applied to the nerve) is called the *exciting or polarizing* current: those which arise in the extrapolar regions, which are the localities influenced, polarized or electrotonized, and in one or other of which two points of derivation are chosen in order to connect them with the galvanometer, are called *derived, electrotonic currents, or currents of polarization.* The region which approximates the anode (positive pole of the battery current) is called *anodic*, and that in the neighbourhood of the cathode (negative pole) is known as *cathodic*. The derived current in each of the respective localities is known as anelectrotonic or *anelectrotonus*, and catelectrotonic or *catelectrotonus*.

1. **Electrotonic currents: direction, duration, intensity.**—*The direction of the electrotonic currents is the same as that of the polarizing current; their intensity progressively decreases in proportion as they are removed from the locality excited in the two extrapolar regions.* These characters suffice to clearly distinguish electrotonic currents from the current of action or negative variation of the nerve, of which the direction is constant, and which is connected with the state of stimulation of the nerve, whatever may be the nature of the stimulus and the direction of the exciting current, when electricity is made use of.

The intensity of the electrotonic currents further varies with the intensity of the polarizing current and the length of the portion polarized. It is not equal for the two localities excited, but anelectrotonus is stronger than catelectrotonus. This intensity is not uniformly maintained during the passage of the polarizing

current, but varies as regards the two extrapolar portions: catelectrotonus at once decreases, while anelectrotonus progressively increases, and then itself decreases.

Interference with the current peculiar to the nerve.—When the middle segment of the nerve is chosen for the space acted upon, as in the experiment which has just been referred to, and one of the extremities for the locality of derivation, this latter is already the seat of a current of definite direction (current of repose or of longitudinal-transverse alteration) whose action is rendered manifest by the galvanometer ; this current reinforces algebraically the electrotonic current, which may be much stronger than itself, and which may be reinforced or weakened by it, accordingly as it has the same or an opposite direction. It is this which was first known as the *positive* and the *negative* phase of electrotonus, an incorrect terminology, inasmuch as the electrotonic current is altogether independent of the current of repose of the nerve. In order to demonstrate it, it is merely necessary to modify the arrangement of the experiment, and to replace the derived portion by the influenced portion, and reciprocally. Derivation, investigated on the median segment of the nerve at two points perfectly isoelectric, presents electrotonic currents when one of the extremities is stimulated, and these currents still follow the same direction as the polarizing current, without any complication of the current special to the nerve.

Rate of propagation.—Electrotonus is transmitted from the portion influenced to the derived portion at a rate which appears to be clearly that of the propagation of the impulses (du Bois-Reymond and Bernstein) : others, it is true, have maintained that its development is instantaneous, like that of the electric current itself. It is in any case very rapid, and hence it is obvious that induced currents may give rise to it just as do the continuous current. Chauveau, Charbonnel-Salle have observed it to ensue after discharges of static electricity.

2. **Paradoxical contraction.**—If, instead of connecting the portion influenced with the wires of a galvanometer, the latter is brought into contact with the freshly cut nerve of a galvanoscopic paw, and electrotonus is produced by the current of a battery or by instantaneous discharges, at every passage of the current, the galvanoscopic paw is observed to contract. The physical rheoscope has thus been replaced by a physiological rheoscope which receives the impulses, and these impulses are none other than the electrotonic currents arising in the primary nerve, which reach the cut extremity of the secondary nerve (nerve of the galvanoscopic paw).

The paradox consists in the fact that the excitation of the first nerve seems to be transmitted to the second, in violation of the law of the integrity of structure and of that of isolated conduction.

But this violation is only apparent, because, of these two laws the second applies merely to the nerves which have not been cut, and the first is verified by the fact that, if the two nerves are placed in contact, end to end, contraction does not ensue, the electric differences to which electrotonus gives rise being not produced.

Experiment.—The experiment in its classical form is carried out in the following manner : two principal branches of the sciatic nerve in the frog, these branches being the peroneal and the nerve to the gastrocnemius are prepared, and the trunk of the sciatic is cut in the thigh. If one of these nerves be stimulated (derivations being avoided), a contraction follows not only in its own muscle, but also in the muscle of the other nerve. When the trunk of the sciatic is not cut, the paradoxical contraction would not be obtained, but reflex contractions more or less numerous, which would be recognized by their much longer latent period.

Difference between the paradoxical contraction and the indirect or secondary contraction.—The paradoxical contraction, obtained by putting nerve in contact with nerve, is not comparable to the contraction known as *induced* or secondary,

which results when nerve is brought into contact with muscle (the latter being in a state of contraction).

In this last case, it is the negative variation of the muscle stimulated (by electricity or otherwise) which is the excitant of the galvanoscopic paw; in the first it is electrotonus only and not the negative variation of the electrified nerve which excites the physiological rheoscope. The negative variation of the nerve is much too feeble to give rise to this stimulation; it is for this reason that mechanical or chemical excitation of the nerve is always without effect on the secondary nerve. Electrotonic currents which are susceptible of being much stronger than the negative variation have, for this reason, a definite exciting effect.

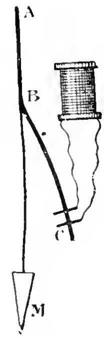


FIG. 41.—Paradoxical contraction.

Let there be a cut nerve trunk AB, whence are given off two branches BC and BM, the latter going to the muscle M. If the branch BC which is not in physiological connexion with the muscle M, be stimulated at C, this latter muscle will be seen to contract.

Several equivalent forms may be given to this experiment and two nerve trunks, of which one is furnished with its muscle, may be coupled together. The only necessary condition is that there should be contact between them for a certain length.

Inequality of the phases.—With equal intensity of the polarizing current, we have seen that the electrotonic currents are unequal; polarization in the region of the anode exceeds that which arises in the region of the cathode, independently of the current of repose, which is diminished or reinforced according to the direction of the polarizing current; it thus follows that when alternating currents which are equal and not too strong succeed one another with a certain frequency, the resulting effect will manifest itself by a feeble anelectrotonic current. This current must not be confounded with the negative variation, such as may itself arise from the employment of the so-called tetanizing currents. Charbonnel-Salle has proved that the electrotonic state may be induced by short currents by the aid of the electrometer of Lippmann, and has also proved that, in these conditions, the same regulative laws are in action as when it is produced by continuous currents.

Difference between electrotonus and negative variation.—Electrotonus and negative variation have this in common, that they are transmitted, both of them, through the length of the nerve outside the portion influenced by the exciting current; both depend on the integrity of the structure of the nerve, and they disappear when the latter has been tied or crushed between the portion influenced and that which is derived. On the other hand, they are distinguished from each other by the three following characters: (1) the electrotonic modification may be demonstrated by connecting two isoelectric points of the nerve to the galvanometer, while negative variation is only observed when two points of a different potential are thus connected; (2) *the electrotonic modification progressively decreases with the distance between the portion influenced and the derived portion, while the intensity of the negative variation remains the same whatever length of nerve may be interposed between the point excited and the extremity on which the derivation is taken*; (3) electrotonic variation is definitely related to the direction of the influencing current, while negative variation has a direction independent of that of the current made use of to excite the nerve.

3. **Theories of electrotonus.**—The electrotonic current originates in a polarization which the exciting current produces in the extrapolar regions. This polarization is differently interpreted by different authors.

Some, as du Bois-Reymond, regard it (although connected with the special

structure of the nerve) as being of purely physical nature, and of the same kind as that, though much more complicated, which is presented by the molecules of soft iron when a current is made to pass through the latter ; others, as Matteucci, Hermann, look upon it as the result of the chemical phenomenon of electrolysis due to the difference of electrical conductivity of the different parts of

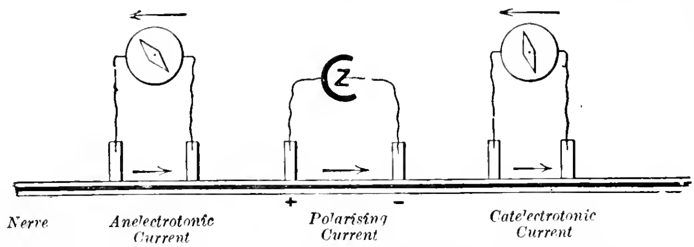


FIG. 42.—Polarization of the nerve in its two extrapolar segments and production of electrotonic currents in these two segments.

The middle region is traversed by a constant current (polarizing current). The extrapolar regions show currents of polarization of the same direction as the preceding, but unequal in intensity. The anelectrotonic current is more intense than the catelectrotonic current.

the nerve, or rather of the nerve element, the axis cylinder being a much better conductor than the myelin. If a current is sent through the badly conducting investing sheath, at the point of contact with the two bodies a polarization arises (the opposed current increasing the resistance to the passage of the current from the sheath to the axis cylinder). On account of this resistance, the current spreads to right and left from its point of application to the ramifications, and distributes genuine derived currents having the same direction as the current of the battery, and which progressively diminish in intensity in proportion as the distance from the points of application of the principal current becomes greater ; these are the currents which are received by the galvanometer connected with the nerve and which represent the electrotonic currents.

Nerves of different structure.—In the non-myelinated nerves electrotonus is generally wanting (Biedermann) ; yet this absence is not total (Boruttau) ; the

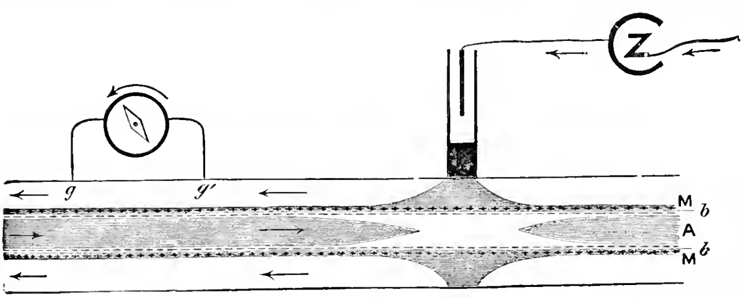


FIG. 43.—Internal polarization of a nerve fibre, giving rise to an electrotonic current in the extrapolar region. Only one of the influencing poles is represented (after Waller).

A, axis cylinder ; MM, myelin ; *bb*, surface of contact between A and M, where it is supposed that the polarization gives rise to a resistance which obliges the current to diffuse itself following this surface. The intensity of the polarization progressively diminishes, starting from the point of application of the pole under consideration of the influencing current.

difference is merely quantitative (Mendelssohn), qualitatively the phenomena are the same.

The non-myelinated nerves, generally little experimented upon, are thus parti-

cularly well adapted for the study of negative variation without the complication of electrotonus.

Integrity of structure. Electrotonus disappears when the nerve is crushed between the portion influenced and that derived, as Longet has observed.

Schematic reproductions. — By means of special apparatus, it is possible to reproduce the principal phenomena of electrotonus, as has been done by Matteucci, Gruenhagen, Hermann. And it may be maintained that the essential and very simple conditions of these schemes are reproduced in the nerve ; but others also arise in this latter by which electrotonus is assimilated to the manifestations of organized tissues.

It is thus that this phenomenon disappears in the case of the dead nerve, and when the latter has degenerated (Schiff, Valentin), that it diminishes or disappears for a longer or shorter time under the influence of anæsthetics (Waller, Biedermann).

Consecutive effects.—Post-electrotonic current. — Before wholly disappearing at the breaking of the polarizing current, electrotonus is first followed by an inversion of the direction of the current (Fick), which is clearly demonstrable only in anelectrotonus (Hermann).

2. Electrotonus. Modifications of Excitability.—*The polarizing current*, whose effects are exerted either on the interpolar region or on the neighbouring localities situated outside its poles, causes in it *similar local modifications of excitability*, whose general tenor has more than one relationship to the physical effects which are produced by it. In order to study these modifications, the nerve is left in connexion with its muscle ; by its other extremity it may be connected or not with its centre. The polarizing current passing through its middle or *interpolar* segment, the extrapolar segment in connexion with the muscle will be described as *myopolar ;* the other will be called *centropolar*. When the influencing current follows the same direction as that taken by the impulses which proceed to the muscle, it will be called *descending :* the cathode (negative pole) is then on the side of

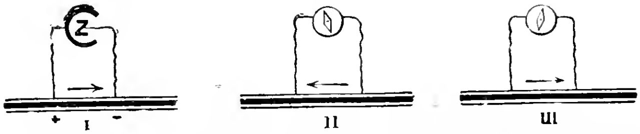


Fig. 44.—Post-electrotonic intrapolar currents produced after the cessation of the polarizing current (after Waller).

I, polarizing current ; II, ordinary post-current of contrary direction ; III, post-current whose direction is the same as that of the polarizing current.

the muscle and the myopolar segment is in a condition of catelectrotonus ; while the anode (positive pole) is on the side of the centres and the centropolar segment is in a condition of anelectrotonus. On the other hand, it is called *ascending* when the cathode and the segment in a state of catelectrotonus are on the side of the centre ; the anode and the segment in a state of anelectrotonus, on the side of the muscle.

Proof of Excitability.—The local excitability of the different points of the different segments will be investigated before, during and after the passage of the influencing current. By experimenting with short excitations, the increased or diminished effects of the latter will then be demonstrated by muscular contractions, which may be registered in order that they may be compared one with another. In the extrapolar regions, electric stimulation may be applied without any difficulty by means of induced currents ; in the intrapolar region, this excitation may be effected either by electricity, certain precautions being taken so that the polarizing current be not deranged, or mechanically or chemically.

Sketched out and successively investigated by Ritter, Nobili, Matteucci, Valentin, and formulated as regards its essential points by Eckhard, the study of electrotonus has been completed and perfected by the extensive and very methodical work of Pflüger.

General formula.—If it be assumed that the middle portion of the nerve be traversed by a current whose intensity is described as medium, the excitability of the nerve is modified throughout its extent. *It is increased in the neighbourhood of the negative pole* (cathode) : *this is catelectrotonus ; it is diminished in the neighbourhood of the positive pole* (anode) : *this is anelectrotonus.*

The nerve is thus, as it were, divided into two regions, the one of increased excitability, the other of diminished excitability ; these regions being separated by a point called *neutral* or *indifferent*, situated in the intrapolar region, which preserves its initial excitability.

Positive and negative modifications.—The modification, whether positive or negative, attains its *maximum* at each pole (positive at the negative, and *vice versa*) and thence progressively decreases in the neighbouring extrapolar region, as also in the portion of the intrapolar region which is adjacent to the pole in question. A curve in the form of an S placed horizontally, surrounding the nerve as an axis, expresses, in a sufficiently graphic manner, these modifications, save that the extremities are strongly inflected on the outside, the decrease of the modification being effected by a much more gradual incline in the extrapolar regions than in the intrapolar region.

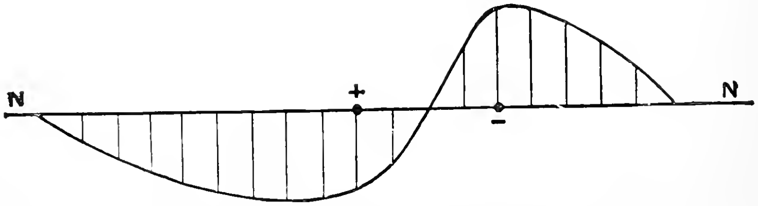


Fig. 45.—Diagram representing the contrary variations of excitability in the regions adjacent to the negative and positive poles.

NN, nerve to which are applied the two poles of a constant battery. The two inverse variations are never exactly symmetrical. When the current is strong, there is a tendency to the invasion of the whole nerve by anelectrotonus. The neutral point becomes more and more displaced towards the negative pole. When the current is feeble, this displacement is made in the opposite direction.

A. medium current.—In the current which is known as *medium*, this curve is almost symmetrical ; and the current is called medium *by definition*, when the inverse modifications of the excitability assume this symmetrical form. As regards intensities which are superior or inferior to that which gives this result, the curve assumes slightly different forms, which are characterized, not merely by the stronger or weaker inflections towards the poles, but also by the displacement of the neutral or indifferent point, in one or other direction. This displacement, which is the greater in proportion as the current is stronger or weaker, gives to the curve that unsymmetrical form which has been mentioned above. In the case of *weak* currents, the neutral point approximates the anode, and hence relatively increases the excitability, in one word, causes the catelectrotonic condition to predominate ; in the case of *strong* currents the contrary happens : the neutral point is displaced towards the cathode and the anelectrotonic condition predominates, and tends to occupy the whole nerve.

Ascending and descending current.—According as the current is ascending or descending, these modifications are, in each case, of opposite denomination. In the case of the ascending current, the area of anelectrotonus affects the myopolar segment (that on the side of the muscle) : in the case of the descending current, it is the reverse. As the state of excitability in the nerve is rendered evident by the contractions of the muscle, it is obvious that these contractions will vary in magnitude according to the direction of the current and according to whether the latter is weak, medium, or strong, in conformity with the definition which has been given of these words in the particular case. It has already been pointed out that, in addition to the *intensity* and the direction of the current, the *distance* between the excited point and the polarized region is also a factor ; and regard must also be paid to the *length* of the interpolar region and to the duration of the passage of the current.

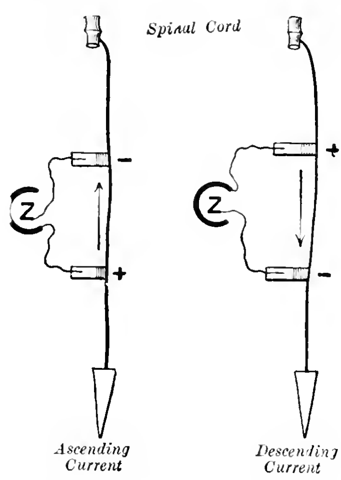


FIG. 46.—Diagram of experiment for the study of electrotonus.

Z, battery connected with motor nerves by two non-polarizable electrodes. Between the two poles is the interpolar segment ; below, the myopolar segment with its muscle ; above, the centropolar segment. In the diagram on the left, the current is ascending ; in that on the right it is descending.

It is the minute study of all the circumstances in their multiple associations that makes Pflüger's work very valuable.

Excitability and conductivity.—Excitability is the more or less marked aptitude of the nerve to receive locally the exciting impulse; conductivity is the greater or less aptitude of the nerve to transmit this impulse along its length to the muscle. The modification of both these aptitudes has one and the same consequence: that of increasing or diminishing the magnitude of the contractions. The analysis of special cases proves that it is now to one, now to another of these two modifications that the change observed is due.

B. *Strong current.*—Let it be assumed that a strong or very strong current influences the middle region of the nerve, and that this current is descending, excitability will be considerably increased in the area approximating the negative pole, and consequently in the myopolar segment; the least excitation of this region will provoke strong contractions; on the other hand, excitability will be greatly reduced in the centropolar segment, and stimulation of this segment, especially in the immediate neighbourhood of the positive pole, will remain without effect. Here the local excitability is increased on the one side and diminished on the other.

Let it be supposed, on the other hand, that this same current is ascending. The catelectrotonic and anelectrotonic areas are inverted. The myopolar segment is anelectrotonized, and its stimulation yields no contraction, because its local excitability is extremely diminished. The centrapolar segment is catelectrotonized; but, in spite of the local excitability of this segment being augmented, it yet gives no evidence of this, because the transmission of the impulse is arrested in the anelectrotonized myopolar region. This univocal manner in which excitability and conductivity comport themselves with regard to electrotonus is a strong argument in favour of their identity.

Anelectrotonus and inhibition.—The stoppage of the contractions due to anelectrotonus has often been compared to the result of inhibition, so much so, indeed, that these two phenomena have been completely assimilated. If by inhibition is implied every arrest due to the intervention of some force, this view is correct; but it is necessary to remember that the phenomena usually described under this name, the stoppage of the heart by stimulation of the vagus, and a number of other more or less analogous phenomena, are caused, not by a special form of action of a stimulus on a nerve, but by *the action of the nerve on other nerves, an action, further, which is provoked by a trivial excitation.* If the phenomena of inhibition be generalized, it is imperatively necessary to define categories in the disparate whole formed by the facts which are comprised in them. In the meantime, there is nothing to prove that the inhibition of one nerve by another is due to an anelectrotonic action of the terminal pole of the second on the initial pole of the first.

C. *Weak Current.*—In proportion as the intensity of the polarizing current decreases, the catelectrotonic action tends to increase relatively to the converse action, and it may predominate over it. Thus with more feeble currents may be obtained contractions either with the ascending or with the descending current.

Electrotonus in man.—Since Helmholtz, a large number of authors have attempted to reproduce electrotonus in man, but generally with variable, uncertain and paradoxical results. Waller and Watteville have demonstrated that excitability is increased at the anode and in the anodic region, while it is diminished at the cathode and in the cathodic region. In other words, electrotonus follows the same rules in man and in animals.

DIFFERENT CONDITIONS WHICH INFLUENCE ELECTROTONUS.

			Direction of the current in relation to the physiological conduction of the nerve.	Influence of the intensity of the polarizing current.	Initiation and consecutive effects.	Influence of the length of intrapolar region.
I.—EXTRAPOLAR REGIONS.	ASCENDING CURRENT.	C. J.	(Centropolar segment.) *Extrapolar ascending catelectrotonus.*	The effect first increases then diminishes and is inverted.	Rapid initiation; leaving after it a positive modification, preceded by a short negative phase.	The effect first increases then becomes nil, and is inverted.
		C.	(Myopolar segment.) *Ascending extrapolar anelectrotonus.*	Effect increases progressively without change of sign.	Slow initiation; maximum obtained after several minutes.	Effect increases without changing sign. (Slower than for intensity.)
	DESCENDING CURRENT.	C. J.	(Myopolar segment.) *Descending extrapolar catelectrotonus.*	Effect goes on increasing.	Rapid start, slow, increase; leaves a negative modification, then a positive modification, which disappears.	Effect grows rapidly.
			(Centropolar segment.) *Descending extrapolar anelectrotonus.*	Effect increases progressively without change of sign.	Slow initiation.	Effect increases without change of sign.
I. INTRAPOLAR REGION.	ASCENDING OR DESCENDING CURRENT.	C. J.	The length of the intrapolar polarized region has no effect on its own excitability. The extension of the modification is limited by the situation of the poles. The modification is positive near one and negative near the other. A neutral point of unaltered excitability exists in the interval between the poles. With the augmentation of intensity of the current, this point is displaced from the anode towards the cathode (consequently in the direction of the current). According to the situation of this point the total excitability of the intrapolar area is augmented or diminished. Whatever be the direction of the current (but especially ascending) it will be seen that with weak currents this total excitability is first augmented, little by little attains a maximum, and is then diminished.			

3. **Law of contraction**—In the scheme which has just been given, the modifying action is supplied by a current (continuous), while the exciting action is effected by another current (induced), by means of which the different portions of the nerve under examination are investigated. But the battery current at the instant that it is directed through the nerve produces an excitation, and when it is broken another excitation is brought about, in accordance with the laws governing the origin of the excitation. When a graduated series of makings and breakings of the continuous current is carried out on a nerve, whether ascending or descending, a series of excitations and of modifications of excitability is all at once initiated whose effects (muscular contractions) are explained by the laws formulated above.

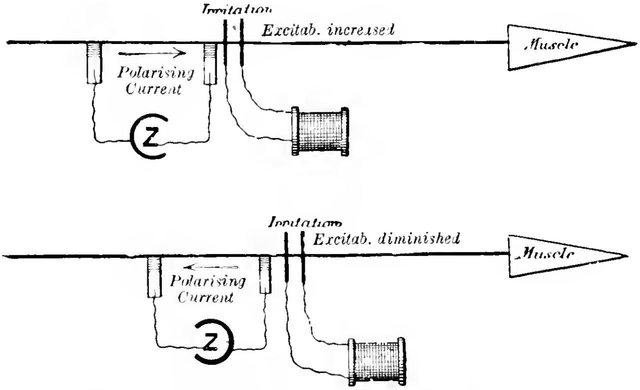


FIG. 47.—Determination of excitability of the myopolar segment during the passage of a current through a certain length of the nerve.

In the upper figure, the polarizing current is ascending, excitability is diminished in the myopolar segment. In the lower figure the polarizing current is descending, the excitability of the myopolar segment is increased (after Waller).

Diagrammatic table.—The results of these series may be systematized in the following table.

Current.	Descending.		Ascending.	
	Make.	Break.	Make.	Break.
Weak.	Contraction.	—	Contraction.	—
Medium.	Contraction.	Contraction.	Contraction.	Contraction.
Strong.	Contraction.	—	—	Contraction.

Discussion.—As is thus seen, the weak current causes two contractions at its making, whether it be descending or ascending. The medium current causes four contractions. The strong current once again brings about two, the one at

the making of the descending current, the other at the breaking of the ascending current. An explanation of the absence of the contractions which are missing must be sought for.

(a) *Weak current.*—As regards weak currents, the two breaking contractions are wanting on account of the weakness of the current, the exciting action of the break being regarded as inferior to that of the make, possibly in consequence of the alteration which is produced by the passage of the current.

(b) *Strong current.*—As regards the strong current, the absence of the breaking contraction of the ascending current is due to the marked effect of anelectrotonus (diminution of excitability) in the portion of the nerve which is in proximity to the muscle and in contact with the positive pole. On the other hand, the very considerable magnitude of the breaking contraction of this same ascending current is due, after the cessation of anelectrotonus in this region, to a contrary modification, which acts like catelectrotonus by augmenting excitability. *After the cessation of the passage of the current from the battery, an after current of opposite direction is indeed developed in the nerve* (for many reasons, amongst others, electrolysis), as in every polarized circuit. Lastly, the absence of the breaking contraction in the case of the descending current is explained by the establishment of an after current of the same kind which, after the cessation of catelectrotonus developed by the passage of the polarizing current, gives rise to the development of a contrary modification equivalent to a strong anelectrotonus.

(c) *Medium Current.*—As regards the medium current, the exciting effect of breaking is now sufficient to bring about an excitation, and on the other hand the anelectrotonic modifications, both direct and consecutive, are still sufficiently feeble not to hinder the occurrence of the contraction ; hence four contractions—two on making and two on breaking of the two currents.

Electrotonic theory of excitation.—On the strength of these facts, Pflüger gives the following formula of electric excitation : *Excitation arises through the production of catelectrotonus or through the cessation of anelectrotonus.*

Tetanus produced by the continuous current.—When a considerable extent of the nerve is traversed by a continuous current (especially a descending current), during its passage a continued contraction—a tetanic muscular contraction—may be produced.

Breaking tetanus.—Conversely, when the ascending current is strong and is long continued, it may produce, on breaking, instead of a shock, a tetanic contraction similar to the preceding. These apparently tetanic contractions appear to be inordinately prolonged shocks, such as are obtained when the nerve or the muscle is fatigued or subjected to the action of cold or certain poisons (veratrine). Neither making nor breaking tetanus (Hering and Frederick) causes secondary tetanus in the galvanoscopic paw.

Volta's alternatives.—For seen by Ritter, incompletely formulated by Volta, the law governing these phenomena has been expressed in the following manner by Rosenthal and Wundt : *The continued passage of a current of a given direction increases the breaking excitability of the current of the same direction and the making of the current of the opposite direction ; it weakens it as regards the making of the first and the breaking of the second.* If the existence of an after current of polarization is admitted, and if the so-called breaking contraction be attributed to the making of this inverse current, the law becomes simpler and may be formulated thus : *the passage through the nerve of a current of a given direction increases the excitability of this nerve for a current of the opposite direction.*

Succession of effects with weak currents.—According to the authors who have studied it, and according to the point of view which each of them has adopted, the law of contraction assumes a particular form, as is shown by the tables which have been prepared to express it. Its main outlines are sketched in Pflüger's

table. That of Heidenhain expresses in detail the increasing effects of weak currents, until they attain the intensity which is known as medium.

Current.	Descending.		Ascending.	
Intensity.	Make.	Break.	Make.	Break.
I. . . .	—	—	Contraction.	—
II. . . .	—	Contraction.	Contraction.	—
III. . . .	Contraction.	Contraction.	Contraction.	—
IV. . . .	Contraction.	Contraction.	Contraction.	Contraction.

Disappearance of contractions as the nerve gradually perishes.—The following table, due to Nobili, expresses the action of another condition, that of the *variation of excitability of the cut nerve* which belongs to a separated limb of the animal. This assumes that the stimulations are no longer extemporaneous, but succeed one another at long intervals, leaving to time the task of performing its work. The excitability of the nerve at first progressively increases ; then it regularly decreases, and this decrease is rendered evident by the gradual disappearance of the contractions one after the other. In the case of a nerve having its maximum excitability it would be as follows :

Degree of Excitability.	Descending Current.		Ascending Current.	
	Make.	Break.	Make.	Break.
I. . . .	Contraction.	Contraction.	Contraction.	Contraction.
II. . . .	Strong contraction.	Weak contraction.	—	Strong contraction.
III. . . .	Strong contraction.	—	—	Strong contraction.
IV. . . .	Contraction.	—	—	—
V. . . .	—	—	—	—

Law of Ritter-Valli.—This table expresses the variations of nervous excitability regarded in their *succession in time.* It should be added that this loss of excitability is not total ; it does not involve the nerve in its entirety, but follows a progression *in the direction of its length.* In the motor nerve it first affects the extremity which is farthest removed from the muscle, and then progressively involves the portions of the nerve which are nearest to the former. This mode of disappearance of excitability is the same whatever may be the nature of the alteration which produces decay of the nerve (anæmia, curare, Cl. Bernard ; local anæsthesia, Ioteyko and Stefanowska). In sensory nerves, whose conduction is the converse of that of the motor nerves, the progress of the loss of excitability is inverted, and proceeds from the periphery to the centres. (The same authors.)

Electrotonus in the monopolar applications of electricity.—A nerve may be excited, as Chauveau has shown, by placing a single electrode of the current on it, while the other electrode is placed on a remote region (more or less symmetrical). It hence follows, without any possible error, and contrary to that which Hermann maintains, that electrotonus (in other words, the modification of excita-

ability which accompanies the electrotonic currents) may and should arise in these conditions (Morat and Toussaint). Clearly the results of this mode of a unipolar application of electricity must be connected with those of bipolar application, and this connexion is made manifest by arranging, as I have done, in a parallel table the results obtained by these two methods of operating. A knowledge of this concordance is the more useful inasmuch as if bipolar application is almost exclusively employed in physiology, the unipolar method is the only possible and correct one clinically; hence it is necessary to make sure of the equivalence of the two methods in order that clinical practice may benefit from experimental results.

From the theoretical point of view, for the explanation of the effects of electricity, this comparison is also not without interest. It proves to demonstration that the specific nature of the action for a long time attributed to the direction of the current, really belongs to the nature of the pole in contact with the stimulated nerve (in the unipolar method), with the myopolar portion of the nerve (in the bipolar method). This is markedly shown in the following table, in which the succession of effects due to an increasing intensity of the currents in the two modes of excitation is noted.

FIG. 48.—Progressive loss of excitability in the cut motor nerve.

The points A, B, C, D become successively inexcitable after having undergone a slight phase of hyperexcitability.

	CURRENT.	MAKING.	BREAKING.	POLE.	MAKING.	BREAKING.
WEAK.	Ascending	Contraction	—	Negative	Contraction	—
	Descending	—	—	Positive	—	—
	Ascending	Contraction	—	Negative	Contraction	—
	Descending	Contraction	—	Positive	Contraction	—
MEDIUM.	Ascending	Contraction	—	Negative	Contraction	—
	Descending	Contraction	Contraction	Positive	Contraction	Contraction
	Ascending	Contraction	Contraction	Negative	Contraction	Contraction
	Descending	Contraction	Contraction	Positive	Contraction	Contraction
STRONG.	Ascending	Contraction	Contraction	Negative	Contraction	Contraction
	Descending	Contraction	—	Positive	Contraction	—
	Ascending	—	Contraction	Negative	—	Contraction
	Descending	Contraction	—	Positive	Contraction	—

Electrotonus in nerves of different functions.—Electrotonus, in so far as it is a modification of the excitability, is an absolutely general property of the nerves, just as is excitability itself, or the conduction of the impulses, and which manifests itself, like the latter, independently of the special functions of these nerves. The functions of nerves depend on their connexion with nervous or non-nervous elements, which they govern, or from which they receive the impulse.

(a) **Secretory nerves.**—If, instead of a motor nerve, a secretory nerve be stimulated, in place of a muscular contraction, there will be a flow of liquid from the gland. The law of contraction may be verified in these new conditions, as Biedermann has shown. This author, operating on the glosspharyngeal of the frog, and the nerves of the tongue, has found it advantageous to estimate by the galvanometer the current of secretion, rather than the secretion itself.

(b) **Inhibitory nerves.**—By stimulating the pneumogastric, which is the type of inhibitory nerves, by continuous currents of varied intensity and direction, Donders has been able to prepare a table of the law of contractions similar to that of Pflüger, except that in it contraction is replaced by arrest of cardiac action, and repose or want of contraction by the continuation of the movement of the heart.

(c) **Elements of association.**—The inhibitory nerves are not terminal neurons, like those of the anterior roots proceeding to the muscles of the skeleton ; by definition they are considered as associating elements whose function, determined by their special connexion with the motor elements properly so called, terminates in this apparently strange phenomenon, the arrest of movement. The internal elements of the nervous system (intercentral elements) thus present the phenomenon of electrotonus. This is equivalent to saying that the phenomena of electrotonus appertain to every nervous element.

Sensory nerves.—The initial nerves, like those which are terminal and the intercentral nerves, should present electrotonic modifications. In such nerves, and for reasons which are readily understood, these phenomena are not easily to be detected in animals, on whom we can only measure sensibility under its reflex form, and by no means without difficulty (Zurhelle).

Nerves of special sense—In man this study has been undertaken on the nerves of special sense.

(a) *Taste.*—The passage of a current through the tongue produces a sensation of taste, acid at its entry, alkaline (almost bitter) at its exit (Pfaff, Volta and Ritter).

(b) *Sight.*—A current proceeding towards the ganglionic cells (descending current) causes the sensation of darkness ; a current proceeding in the opposite direction (ascending current) causes a sensation of light (Helmholtz).

(c) *Hearing.*—It may be shown, but not without difficulty, that the law of contraction is applicable also to the sense of hearing (Brenner).

Polar influence on non-differentiated protoplasm. — Kühne was the first to demonstrate the action of electricity on the non-differentiated or but slightly differentiated protoplasm of the lowest animals. Verworn has made a methodical study of this action. It is generally held that the protoplasm of the unicellular beings represents living matter under an elementary form and apart from all the structures which are superposed on it in the more highly organized beings.

Hence it has been supposed that the response of such a substance to excitants would be equivalent to that of the least differentiated cells of superior animals, and even to that of the least differentiated substance which exists in these cells ; that, in a word, it should be univocal and very simple in its expression. As a matter of fact, the response to electrical excitations of unicellular beings is somewhat complicated. This result appears to indicate that the comparisons or assimilations made between beings of different organization are not perhaps very accurate. The simplicity of monocellular beings (amœbæ, infusoria, etc.) is not so great as has been supposed and, above all, its mode of expression is otherwise than that which has been held to be the case. In the amœba all the essential functions of life are already represented, but, in a sense, undivided, in its protoplasm. In the course of phylogenetic evolution, a distribution of atri-

butes is made between the different portions of this protoplasm, a division in virtue of which each one of them increases its aptitudes in a given direction, for the performance of a given function, while it loses its aptitudes in an opposite direction, to the gain of other differentiated portions with regard to other functions. Hence evolution, differentiation, results at the same time in the attainment of a greater perfection of the functions of the whole, and in a specialization, that is to say, a reduction of the functions of the part, hence the inability of the latter to live by itself when it is detached from the whole to which it belongs.

Galvanotropism.—An amœba, placed in a drop of water through which a current is passed, reacts under the action of this current. *The portion turned towards the anode* (positive pole) *is retracted, while that facing the cathode* (negative pole) *is protruded* and forms a pseudopodium. If the current be reversed, the same phenomena occur, but in the converse manner. Hence, under the action of the two opposite poles, a double inverse deformation occurs. Which of the two is the equivalent of a muscular contraction ? It is very difficult to decide. In a definite differentiated protoplasm, such as that of muscle, nothing is more clear than the contrary state of repose and of contraction. But in the diffuse protoplasm of the amœba, the direction of the forces varies according to circumstances. As a matter of fact, both changes of form practically arise at one and the same time from a contraction in one direction, and a compensatory protrusion in the other. Retraction is always the active phenomenon. When the force is parallel to the pseudopodium, it causes it to retract ; when it is circular and perpendicular, it causes it to elongate. In both cases there is an expenditure of energy ; in both cases there is a contraction, and from a certain point of view the phenomenon is less simple in the amœba than in the muscular fibre. That which is remarkable is, that the anode excites one of these movements and the cathode the other, in a predominant or special manner.

Yet, a double converse deformation, such as that which has just been described, implies a tendency to locomotion. Certain unicellular beings, ciliated or not, present, under the influence of the current, a change of place to which the name of *galvanotropism* is more particularly applied. Electrotonus, the reactions of excitable substances varying according to the nature of the pole, or the direction of the current, are merely varieties of galvanotropism.

E. DIFFERENT USES AND EFFECTS OF ELECTRICITY

Action of the magnetic field ; electric waves ; electric rays.—When a current is projected into a circuit, lines of force are developed around this latter which create around it a field of force, known as the *magnetic field*. If another circuit is placed in this field of force (in an appropriate position), induction occurs, electric movement in this second circuit. If, instead of this second circuit, an excitable tissue be placed in the magnetic field, as the galvanoscopic frog's foot, what will happen ? This question has been studied by several authors, more especially by Danielewsky, and more recently by Radzikowsky.

As a matter of fact, *when a frog's nerve is placed in a field of force, it is excited by the variations of the intensity of this field.* In this tissue, the structure of which is very complicated, it may be admitted that induced currents are developed which arouse to activity its very excitable substance. In certain positions of the nerve the stimulation is at its maximum, for example in that in which it is placed in the same plane as the inducing circuit and perpendicular to an element of this circuit, the muscle being turned to the outside. The arrangement of the experiment may be greatly varied, and the nerve may be placed in the field in the neighbourhood of one of the isolated poles (unipolar excitation). The nerve must be isolated ; if it is left in position surrounded by other tissues, or if, after

it has been laid bare, it is covered with a conducting envelope, it will no longer be subjected to the action of the field of force. The surrounding tissue acts as a shunt (Radzikowsky) or, to speak more precisely, as a screen (Danilewsky).

Electric opacity and transparency.—If, indeed, some conducting body be placed in the magnetic field so that it crosses the line of progress of the electric waves (a plate of metal, the hand), the excitation by induction ceases; the interposition of a dielectric (a glass plate) allows the waves to pass. The conductor is *opaque* to the electric waves (as to luminous rays): the dielectric, which is often known as the isolating agent, is *transparent* as regards these rays.

Electric immunity.—It will thus be understood that tissues which are but little excitable, but which conduct electricity, help to render the more excitable tissues irresponsive to the action of the magnetic field, which is created around them by the electric phenomena developed in the organism. In the same way, as regards an excitable cell or fibre, a conducting envelope may preserve it from the excitation which would arise from this cause. In order to protect living elements against stimuli which are not intended for them, there would thus be two methods available: the one consists in surrounding them with *dielectrics* which preserve them from excitation by conduction, the other consists in surrounding them with *conductors* which prevent their being excited by induction. The same element may make use of these two methods. This special organization allows the element to reject the excitation in certain of its parts, and to receive it in certain other points of election.

High frequency currents.—The so-called high frequency currents are those which attain the number of 500,000–1,000,000 per second. Their action has been studied on living beings, partly by direct application, partly by placing the subject in a solenoid, which creates around it a field of force (d'Arsonval).

(a) *Direct action.*—The very high frequency of these currents confers a kind of immunity at the site of their passage on the organism which they traverse. At an equal voltage, they are infinitely better supported than currents of an ordinary rhythm (say 100 to a second). However, by augmenting the intensity, they may be rendered injurious, and death may ensue in animals (Bordier and Lecomte).

(b) *Indirect action through a field of force.*—When an animal is placed in the interior of a solenoid in which such currents circulate, an augmentation of the respiratory exchanges is observed (d'Arsonval). This influence on the exchanges is nevertheless not due to the special action of the induced currents acting on the nervous system, or the tissues, but is a secondary effect attributable to the heat developed by the current. It is known, indeed, that heat by itself increases the activity of the exchanges, when it becomes increased to such an extent that the animal scarcely resists it.

Death by electricity.—Prevost and Battelli have made a special study of the mechanism of death by electricity and the conditions which give rise to it as regards the electric agency. They have experimented on dogs, rabbits, guinea pigs and rats, by sending a current

through the body from the head to the anus. The resistance of the animal varied from 400 to 900 ohms. The duration of the application varied from some hundredths of a second to two or three seconds. The results differ according to the animal. The authors have investigated the action both of continuous and of alternating currents.

(a) *Alternating currents.*—These currents must be divided according to their tension into those of *low tension* (10 to 120 volts), those of *medium tension* (about 620 volts), and those of *high tension* (1,200 to 4,800 volts).

With currents of low tension a *stoppage of the heart with fibrillary tremor* is observed in the dog. Respiration continues for some minutes, but in its turn ceases by anæmia of the medulla oblongata. The animal dies. The rabbit and the rat offer a much greater resistance. Sometimes 10 volts will suffice to kill a dog.

Currents of medium tension produce, in the dog, a stoppage of respiration as also of that of the heart. In other animals stoppage of respiration is usually alone observed; further, there is generalized tetanus and anæsthesia.

Currents of high tension cause, in all animals, stoppage of respiration, while the heart continues to beat. In this case animals may be saved by the use of artificial respiration. But when, on the other hand, the heart stops first, artificial respiration is altogether ineffective.

(b) *Continuous current.*—These currents have been raised up to 540 volts. Although breaking is more dangerous, accidents are not exclusively due either to making or to breaking. Further, the phenomena differ but little from those which are observed when alternating currents are made use of.

Other things being equal with regard to tension, when alternating currents are made use of, the number of interruptions to the second forms an important factor. This has been made to vary from 9 to 1,720 to the second. A rhythm of 150 the second is that in which death is least likely to occur. Below, but especially above this number, the voltage must be considerably increased for the same effects to be produced. A continuous current acts like an alternating current of the same voltage at 350 to the second.

It is a curious fact that the heart which has been stopped by a low tension current may once again be set in action by a high tension current.

The results to which these experiments lead are somewhat different from those which are generally accepted.

Mechanism of death.—According to the nature of the animal, according to the voltage of the current, according to its rhythm if it is alter-

nating, the first stoppage may affect either respiration (high tension), or the heart (low tension). The stoppage of the heart is clearly the only cause of death, inasmuch as artificial respiration is possible, and the normal respiration may spontaneously be renewed, which does not occur in the case of the heart.

Currents of medium and low tension should then be more dangerous than those of high tension. As a matter of fact, when *death ensues* it is always *by stoppage of the heart.* Artificial respiration should, nevertheless, be attempted and persevered in.

The observations which have been made in cases of death from accidents arising in the industrial applications of high tension electricity must be regarded as being contradictory; the tension of the current to which the victim has been subjected, by derivation or otherwise, not usually being that of the direct current which circulates in the line, but usually much weaker, its exact strength being indeterminate.

F. NERVE POISONS

Cl. Bernard was the first to analyse the tissues and their functions by means of poisons, which for this reason he called the "reactives of the physiologist." In this order of investigation he has left examples and methods which his successors can only imitate and make use of without essentially perfecting them. He divides poisons into *general and special*, according as their action affects every cell, or only certain species of cells; or, further, certain varieties of cells, as happens in the case of the nervous system.

1. General poisons—Anæsthetics. — Cl. Bernard regarded anæsthetic substances as general poisons, capable of suspending (without destroying, when their action is not indefinitely prolonged) the activity of all cellular protoplasm. They are for him the *reactives of life.* The germination of cereals, the growth of plants, the movements of the sensitive plant, are arrested by the vapours of chloroform or of ether, as is sensation in animals. In these latter, the movement of the vibratile cilia, the contraction of the muscles, the excitability of the motor nerves, in a word, that of all the tissues, may be paralysed if the tension of the vapours is sufficient and their action sufficiently prolonged. But it must also be added that, between the different species of cells and between the different systematizations which may be effected by them, there are well defined susceptibilities and fairly large gradations, from which it results that in limiting precisely the doses (tension of the vapours) these systems and these elements may be attacked one

after the other; hence arises another form of physiological analysis carried out by the aid of poisons.

The anæsthesia of chloroform and ether.—The action of anæsthetics (chloroform and ether being especially considered) may be divided into three periods, up to the instant when insensibility is complete.

The *first period* is characterized by a sort of drunkenness which, in more than one point, resembles alcoholic drunkenness: vertigo, loss of equilibrium, stimulation of the different senses and of cerebral activity, general excitement. This is the so-called period of excitation, which is never completely wanting, and which should not be confounded with a purely local irritation of the anæsthetic vapours on the upper respiratory tract. The sensations, which are at first exalted, are afterwards dulled and, before consciousness is lost, a condition is manifested of fleeting duration and difficult to obtain and voluntarily maintain, which is yet not anæsthesia, but *analgesia*, and during which painful sensations are alone suppressed.

The *second period* corresponds to a true condition of anæsthesia characterized by insensibility to ordinary painful impressions, as well as those which are not painful, but in which *reflex excitability is entirely preserved*, if not increased. The anæsthetic action should be carried slightly farther in order to ensure the muscular flaccidity which is favourable to operation and to the manœuvres of surgery.

In the *third period*, that of complete anæsthesia, the reflexes of the life of relation disappear, especially the winking of the eyelids consecutively to touching of the cornea, the patellar reflex, the labiomental reflex (Dastre and Loge). The muscles of the limbs are relaxed. The respiratory reflexes, all those which maintain the acts of the life of nutrition and whose sphere lies in the internal organs, are preserved. Not that these functions do not receive the rebound of the toxic action which gradually attacks the nervous system, as is evident by the modifications of the circulation and of the temperature, but the more simple and more resisting systems which govern them preserve their united action to a sufficient degree.

Anæsthetic syncope.—If the intoxication is pushed farther, a serious phenomenon gradually supervenes, menacing life; this is *respiratory syncope*, the stoppage of the movement of respiration which may be combated by the employment of passive respiration artificially maintained by the aid of movements of the thorax. In chloroform anæsthesia cardiac syncope may occur suddenly, and is almost hopeless; further, this accident may occur at the very commencement of anæsthesia. In animals, of which some, like the dog, are liable to this complication, it may be prevented by the previous injection of a small dose (half milligramme) of sulphate of atropine, which diminishes the inhibitory action of the vagus on the heart (Dastre and Morat). This method may be combined with

that of Cl. Bernard, who administers morphine to the animal previously to its being anæsthetized.

During complete anæsthesia, the pupil remains contracted even when the eyelids are closed. At the instant when respiratory asphyxia occurs it abruptly dilates. The state of the pupil should be watched so long as anæsthesia is maintained.

Cocaine.—Cocaine may be classed amongst the general poisons of the nervous system in almost the same category as the anæsthetics. Employed in watery solution, wherever it comes in contact with nerve protoplasm, it suspends or destroys its excitability. Sensory nerves, motor nerves, white and grey matter, all are subjected to its paralysing influence. It is employed locally (clinically) in order to extinguish for a time the sensibility of certain surfaces, such as those of the larynx or the cornea.

Cocaine has been regarded in turn by some (Laborde, Arloing, Laffont) as a special poison, a *sensory curare ;* by others (U. Mosso, Danilewsky, Charpentier) as a general poison, a genuine *anæsthetic.* The first of these two opinions is based on the *local* anæsthetic effect, easily obtained by painting mucous membranes or the skin with a solution of cocaine, while the excitation of sensory nerves which leave these localities, proves them to be very sensitive ; the ultimate ramifications would thus alone be affected and not the nerve trunks, or the cerebral centres. The conclusion is not accurate. It is known, through the example of atropine, that an action which is purely local as regards the pupil after installation into the eye does not exclude the general action of the same substance diffused in the blood, even in a minimum dose. The comparison of the relative weight of the substance employed on the one hand and of the reacting tissue on the other hand, proves, on the contrary (for both poisons) that local action is only produced by large doses, while the general action is obtained by doses which are comparatively very small (say 2 milligrammes per kilogramme in the dog).

The opinion that the substance injected into the blood would only affect the peripheral ramifications of sensory nerves cannot be maintained. A nerve trunk being isolated, it may be subjected locally to the action of cocaine ; it then loses at this point its excitability and its conductivity. The excitations made above the point operated on are no longer transmitted to the terminal sensory or motor organs. This effect at once vanishes with the elimination of the substance. In this manner a delicate means of replacing the section of the nerves is available, and it allows also the complete return of function (two to four drops of the one per cent. solution injected under the sheath of the vagus are sufficient to paralyse it).

The action of cocaine thus applies to all varieties of nerve protoplasm (sensory, motor, voluntary, involuntary nerves, etc.). It also applies to the protoplasm of the muscle. When the substance is brought in contact with the muscles, it modifies their power of contracting (Sighicelli, U. Mosso). The anæsthetic effect, in the general sense of the expression, is displayed in all the branches, whether they have or have not a nervous system (Danilewsky). It hinders the diapedesis of the white corpuscles, without however suspending the chemiotaxis, as does chloroform (Massart and Bordet). It stops fermentation and germination (A. Charpentier).

Thus, therefore, the action is a very general one as concerns all protoplasm, but it is an action which varies unequally according to the nature of the element of the tissue ; it must be added also, that it is an action which varies according to the doses employed (stimulating in a weak dose, paralysing in a strong dose). When diffused in the organism, cocaine gives rise to somewhat complicated effects, like all anæsthetics, but which, on account of their special nature, make

this substance inapplicable as an ordinary anæsthetic, such as is employed surgically. Hence it has been reserved for local application, especially for superficial application, so that there is no danger of marked absorption of this substance causing general effects.

It has been shown experimentally that cocaine acts on the grey masses of the nervous system in the same way as it acts on its terminations or its conductors. When applied directly to the cerebral cortex (motor area), it diminishes its excitability (Charpentier, Carvallo): when injected into a segment of the spinal cord, it diminishes its reflex power (U. Mosso). Gaglio has made use of it in order to study the functions of the semi-circular canals.

When injected into the general circulation, it first attacks the higher functions of the nervous system, and more especially sensation, but it does not produce the dissociation, at the same time regular, prompt and gradual, which gives their therapeutic value to ether, chloroform and nitrous oxide. *Theoretically* it is an anæsthetic, but not *practically* (Dastre).

2. Special Poisons.—Specificity must not probably be taken in the absolute sense of the word. But it may be admitted when it is applied to the action of agents which in infinitesimal doses paralyse certain elements, while in a large dose they leave the properties of others intact. This is the case with curare and with a certain number of substances whose effects are similar or analogous.

Curare.—Curare is employed in an aqueous solution of $\frac{1}{100}$ strength injected usually under the skin or into the veins. According to its quality, its toxicity varies. Curare of good quality produces its ordinary effects in one centigramme doses (one cubic centimeter of the solution of 1 in 100) to the kilogramme of animal injected hypodermically; when injected into a vein, the dose may be diminished by half. In an ordinary-sized frog, two to four drops suffice, injected hypodermically.

Curare paralyses the motor nerves to the exclusion of the other elements of the nervous system and of those of the other tissues. An animal intoxicated by curare becomes paralysed. If the excitability of the nerves and of the muscles is immediately investigated, it is seen that these last respond freely to the electric stimulus, while the stimulation of the motor nerves is without effect.

Intoxication by curare is effected at the terminal extremity of the nerve; in the new phraseology, by the distributing pole of the motor neuron. This may be proved by the following experiment: a frog is taken and a ligature is tightly tied round the loins; thus all communication is prevented by the vessels between the anterior and the posterior portion of the body, but the lumbar nerves are left outside the ligature, and are thus respected. When curare is injected into the anterior portion, the anterior members and the head are incapable of movement; the posterior members on the contrary are not paralysed, and this in spite of the fact that the origins of their motor nerves and the spinal cord itself are bathed in the poison which is diffused through all the parts situated in front of the ligature. If the frog is thrown into water, it swims with its posterior limbs until it reaches the edge of the vessel.

In intoxication by curare the sensory nerves are respected. If in the frog thus

prepared one of the anterior feet, paralysed as regards movement, is pinched, the animal reacts by movements of its posterior limbs.

In intoxication by curare a distinction is made between nerves of animal life and those of organic life. If intoxication is effected with a very small dose, the motor nerves of the skeleton are alone paralysed, the nerves of organic life remain active ; the pupil dilates and contracts, as also the vessels, the stomach, the intestine, etc. But if the dose be increased, these nerves in their turn will be paralysed. The intrinsic nerves of the heart resist the longest and, in cold-blooded animals, the heart preserves its movements even when large doses are given.

Struck by the fact that the paralysis of the motor nerves is only produced in proportion as curare is administered by its muscular ending, Vulpian concluded that this substance acts locally and in an elective fashion on the terminal plate of the motor nerve, the rest of the nerve preserving its properties, but without the possibility of manifesting them, on account of its temporary separation from the muscle. Against this view Cl. Bernard cited the following fact, the knowledge of which is due to him, as that of all the preceding facts. If, during the time that the intoxication is in progress, *the excitability of the different portions of the nerves* be investigated, it is seen that the latter disappears, not totally and at once, but gradually and successively from the spinal cord to the muscle. There is a kind of paradox in the fact that the paralysis commences in the extremity opposed to that by which the poison is supposed to enter into contact with the nerve in order to affect the latter.

A. D. Waller remarks that the different varieties of curare are not identical. Having experimented with *curarine* chemically isolated from curare, he finds that this substance produces motor paralysis like curare, but permits the negative variation of the motor nerve to persist. Thus motor paralysis would be due to a functional dissociation of the nerve and of the muscle, according to the hypothesis of Vulpian. The anæsthetics or general poisons, on the contrary, attack the nerve protoplasm and suppress the negative variation, in other words, the special activity of this protoplasm.

Strychnine.—At the first glance strychnine produces effects exactly the converse to those of curare. Poisoning by strychnine is rendered evident by convulsive attacks, to which the most trifling stimulation of the extremities of the sensory nerves gives rise. This fact is expressed by saying that this substance *increases the reflex excitability of the spinal cord.* When the convulsive attacks are violently repeated a certain number of times, the motor nerves themselves become inexcitable ; this may be partially due to the fatigue of the system which results from over-stimulation. Martin-Magron and Vulpian have nevertheless observed that, when given in large doses, strychnine destroys the excitability of the motor nerves, even if the latter had been previously separated from the spinal cord. This is a fact which must be reckoned with, but it is not of a nature to explain the convulsions at the commencement and which are produced by doses far from large, and which is the striking fact. Knowing, as will be explained further on, that the spinal cord contains both motor and inhibitory elements as regards movement, it is easily understood that medullary hyper-excitability is the result of a paralysing action, *if this paralysis affects unequally the two species of elements, the inhibitory more than the motor.* On the other hand, it is possible to explain how moderate doses of strychnine paralyse the motor nerves of the skeleton without convulsion, when these nerves are separated from the cord, as they do not contain, like the latter, inhibitory elements.

Strychnine would thus be indeed a curare, but one affecting preferably the inhibitory nerves of the animal nervous system, which are hidden away in the interior of the vertebral column, in the cord and the superior centres.

One milligramme of hydrochloride of strychnine suffices to kill an adult rabbit; 2½ milligrammes to 3 milligrammes will kill a moderate-sized dog; 1 centigramme hypodermically, 2 centigrammes taken by the mouth, will place the life of man in danger (Vulpian). *Upas-antiar* has an action closely analogous to that of strychnine, at least as regards certain of its effects (Doyon).

Belladonna, Atropine.—Atropine, like the substances which are still to be mentioned, has an elective action on the vegetative nervous system, and more particularly on certain of its nerves.—As regards the secretory nerves, especially the nerves of sudation and of salivation, it acts like curare, by destroying their excitability, and consequently by preventing the secretion of these glands. As regards the nerves of the heart, it selects their inhibitory elements; it causes a sort of convulsion of the heart, by hastening its beats. In this case, as the inhibitory cardiac nerves (by the pneumogastric) extend away from the vertebral column and are distinct from its motor nerves (contained in the great sympathetic), it has been possible to prove directly that atropine makes them inexcitable.

A half milligramme of sulphate of atropine, injected hypodermically, suffices, in man, to demonstrate the effect of the poison through a diminution of the saliva and sweat secretion and a very slight acceleration of the heart. Substitutes for atropine are *hyosciamine, daturine, duboisine.*

Jaborandi, Pilocarpine.—The effects of pilocarpine are apparently the exact reverse of those of the preceding substance. It paralyses the accelerators of the heart (consequently slowing its beats, which atropine hastens); it convulses the sudoriparous and salivary glands, whose inhibitory elements, it must be allowed, are paralysed. This antagonism is indeed *reversible* or, as is still said, *bilateral*, in this sense that, by the alternative and superposed actions of the two poisons, it is possible to invert the effects a certain number of times (provided that a certain dose is not exceeded). *The antagonism is not between the two substances which chemically neutralize each other, but between the systems of nerves (motor and inhibitory) which oppose one another* in their function, and which the substances attack electively, the one preferably to the other, according to circumstances. Substitutes for pilocarpine are *eserine* and *muscarine.*

Bibliography

Fatigue of the Nerves.—Different Alterations, Indefatigability.—Abelous, *Arch. de phys.*, 1893, p. 437.—Abelous, Charrin et Langlois, *Ibid.*, 1892, p. 721.—Abelous et Langlois, *Ibid.*, 1892, p. 465.—Albanese, *Arch. ital. de biol.*, 1892 et 1893.—Bowditch, *Arch. f. Anat. und Phys.*, 1390, p. 505.—Carvallo, *C. R. Acad. sc.*, 1900, t. CXXX, p. 1212.—Guerrini, *Arch. ital. de biol.*, 1899, t. XXXII, p. 62.—Lambert.—Levy-Dorn, *Arch. f. Anat. und Phys.*, 1895, p. 199.—Marinesco, Sénilité et mort cell. nerv., *C. R. Acad. sc.*, 1900, t. CXXX, p. 1136; Lésions . . ., hyperthermies . . . , 1898, t. CXXVII, p. 774.—Moleschott et Battistini, *Arch. ital. de biol.*, 1887, t. VIII, p. 90. —Monti, Alter. dans inanition, *Arch. ital. de biol.*, 1895, t. XXIV, p. 347.—Pugnat, *C. R. Acad. sc.*, 1897, t. CXXV, p. 736.—Rossi, *Arch. ital. de biol.*, 1895, t. XXIII, p. 49. —Szana, *Arch. f. Anat. und Phys.*, 1891, p. 315.

Currents of Repose, of Alteration, of Demarcation.—D'Arsonval, *Biol.*, et *Arch. de phys.*, depuis 1880.—Becquerel, *C. R. Acad. sc.*, et *Journ. d'anat. et de phys.*, 1870 et 1874.—Bezold (curare), *Arch. f. Anat. und Phys*, 1860, p. 398.—Biedermann, *Sitz. Wien. Acad.*, XCIII, Abt. III.—Du Bois-Reymond, Untersuch. ub. thier. Electr., 1848, et *Archiv.*—Engelmann, *Arch. f. d. ges. Phys.*, XV, 1871, 1877.—Fréderica, *Arch. f. Anat. und Phys.*, 1880.—Galvani, De viribus electricitatis in motu musculari commentarius, *Inst. de Bologne*, 1791.—Grunhagen (curare), *Königsberg. med. Jahrb.*, IV, 1864, p. 199.—Hellwig, Courant axial, *Arch. f. Anat. und Phys.*, 1898.—Hellwig, Axial strom, *Journ. of Phys.*, 1898.—Hering, Theorie der Vorgänge in der Lebend. Subst., *Lotos*, IX, Prag. 1888.—Hermann, Untersuch. z. Physiol. der Muskeln und Nerven, Berlin, 1868; *Handbuch d. Physiol.*, partie I, vol. 2, p. 144, index bibliographique jusqu'à 1879.—De Humboldt, Expér. sur le galvanisme, 1799.—Matteucci, Essai sur les phénom. électr. des anim., Paris, 1844; Leçon sur électr. animale, Paris, 1856; Cours d'électrophysiol., Paris, 1858.—Mendelssohn, Courant axial, *Arch. f. Anat. und Phys.*, 1885; Art. "Electricité" dans *Dict. de phys.*, index bibliographique.—

Morat, Art. "Electrophysiologie" dans *Dict. encyclopéd. des sc. méd.*—Ch. Richet, Physiol. des muscles et des nerfs.—Schift, Lehrbuch d. Musk. und Nerv., *Phys. physiol.*, 1858.—Strong, Physical theory, *Journ. of Phys.*, 1900.—Valentin, *Arch. f. d. ges. Phys.*, I.—Volta, Electricité dite animale, *Ann. de chimie*, 1797–1799 ; Collez. dell. opere, Firenze, 1816.—G. Weiss, Technique d'électrophysiologie, Paris, Masson. Encyclopédie des aide-mémoire.—Wedinsky, *Arch. f. Anat. und Phys.*, 1883.—Wundt, Traité de phys. et mécanique des nerfs.

Negative Variation.—Bernstein, Ub. reflector. neg. Schwank. d. Nerv. strom. und die Reizleit. im Reflexwegen, *Arch. Psychiatr. Nervenkr.*, XXX, 651.—Biedermann, Nerfs sans myéline . . ., *Sitz. Wien. Acad.*, XCIII, Abt. III.—Borruttau, Seuil de la variation, *Arch. f. d. ges. Phys.*, LXV, 1.—Danilewsky, Cerveau . . . C. P. 1891.—Du Bois-Reymond, Untersuchungen.—Charpentier, Oscill. nerveuses, *C. R. Acad. sc.*, 1899, t. CXXI, p. 38.—Engelmann, *Arch. f. d. ges. Phys.*, 1871.—Gotch et Horsley, Excit. centres, *Philosoph. Trans.*, 1891.—Exner, In welcher weise tritt die negat. Schwank. d. spinal ganglion, *Arch. f. Anat. und Phys.*, 1877, p. 567.—Grutzner, *Arch. f. d. ges. Phys.*, XXVIII et XXXII.—Head, Variation négative et variation positive, *Arch. f. d. ges. Phys.*, XL, p. 207.—Hering, *Sitz. Wien. Acad.* LXXXVIII et LXXXIX. —Herzen, *Revue scient.*, série 4, t. XIII.—Hoorweg, *Arch. f. d. ges. Phys.*, LIII et LIV. —Hermann, *Arch. Pflüger*, 1878, t. XVIII, p. 574.—Macdonald et W. Reid, Phrenic, resp. centres, *Journ. of Phys.*, 1898–9, p. 100.—Mendelssohn, Var. cour. axial., *C. R. Acad. sc.*, 1899.—J.-J. Müller, Rapport avec la grandeur de l'excitation, *Unter. phys. Labor.*, Zurich, 1869.—Setchenow, Moelle épin., *Arch. f. d. ges. Phys.*, 1886.—Schönlein, Summation . . . *Arch. f. Anat. und Phys.*, 1886.—Steiner, Temperat . . . *Arch. f. Anat. und Phys.*, 1883.—Tigerstedt, *Arch. phys. Labor.*, Stockholm, fasc. II,—A.-D. Waller, Action des substances toxiques, *Brain*, XIX, 43, 277, 569.—*Journ. of Phys.*, XIX.

Electrotonus.—Baranowski et Garré, *Arch. Pflüger*, 1880.—Bernstein, *Arch. f. Anat. und Phys.*, 1886.—Biedermann, Electrophysiologie, 1895 ; *Wiener Acad. Wissensch.*, 1887.—Du Bois-Reymond, Unters. üb. thier. Electric., 1848 ; *Ges. Abhandl.*, 1859 ; *Berliner Acad. Wissen* et *Arch. f. Anat. und Phys.*, 1859 et suiv.—Bordier, *Arch. de phys.*, 1897.—Brenner, Unters. und Beob. auf d. Gebiete d. Electrotherap. 1869.—Charbonnel-Salle, *Biol.*, 1893 et année suiv., *Arch. de phys.*, 1893 à 1896.—Charpentier, *Biol.*, 1893 et suiv., *Arch. de phys.*, 1893 et suiv ; *C. R. Acad. sc.*—Chauveau, Effets physiol. de l'électr., *Journ. de la phys.*, 1858–1860.—Donders, *Arch. f. d. ges. Phys.*, 1871.—Fick, Unters. üb. electr. Nervenreiz., 1864.—V. Fleischl, *Arch. f. Anat. und Phys.*, 1885.—Gad et Piokowsky, *Arch. f. Anat. und Phys.*, 1893.—Grünhagen, Die electromot. Eigensch. lebend. Gewebe, Berlin, 1873, et *Arch. f. d. ges. Phys.*, 1873. —Grutzner, *Arch. f. d. ges. Phys.*, XXVIII.—Hallsten, Nerfs sensibles, *Arch. f. Anat. und Phys.*, 1880.—Helmholtz, Opt. phys.—Hermann, *Arch. Pflüger*, 1874 et 1879.—Kuhne, Unters. üb. d. Protoplasma, 1864.—Martin-Magron et Fernet, *C. R. Acad. sc.*, 1860.—Matteucci, *C. R. Acad. sc.*, 1838, 1863, 1867, 1868 ; Traité des phénom. électrophysiol. des animaux, 1844.—Mendelssohn, Electrotonus des nerfs sans myéline, *Biol.*, 1900 ; N. sensitif, *C. R. Acad. sc.*, 1884 ; Art. "Electrotonus" dans *Dict. de phys.*, index bibliographique.—Morat et Toussaint, Electrotonus dans l'excitation unipolaire, *C. R. Acad. sc.*, LXXXIV.—Nobili, *Ann. de chimie et de physique*, 1830.—Piotrowski, *Arch. f. Anat. und Phys.*, 1893.—Pflüger, Unters. üb. d. Physiol. d. Electrotonus, 1859.—Regnauld, *Journ. de physiol.*, 1588.—Schiff, Lehrb. d. Muskel und Nervenphys., 1858.—Stewart, *Journ. of Phys.*, 1888 et 1889.—Tigerstedt, Studien üb. mechan. Nervenreizung, *Acta Soc. Fennicae*, 1880 ; *Arbeit. phys. Lab.*, Stockholm, III.—Teschiriew, *Arch. f. Anat. und Phys.*, 1879–1883.—Valentin, Lehrb. Physiol. d. Mensch., 1848.—Verworne, Galvanotropisme ; Act. électr. sur protoplasma, *Allgem. Physiol.*, 1895 ; *Arch. f. d. ges. Phys.*, LXII.—Waller, *Journ. of Physiol.*, 1898.—Waller et Watteville, Electrotonus chez l'homme, *Philos. Trans.*, 1882.—Watteville, Electrot. chez l'homme, Thèse, 1883.—Wedensky, *Arch. de phys. norm. et path.*, 1891.—Werigo, *Arch. f. d. ges. Phys.*, 1885.—Wundt, Unters. z. Mechan. d. Nerven und Nervencentra, 1871.—Zurhelle, Nerfs sensitifs, *Unter. Lab.*, Bonn, 1865 ; Thèse Berlin, 1864.

Anæsthetics. —Arloing, Thèse doctorat, Lyon, 1879 ; Identité des conditions pour obtenir l'anesthésie générale dans les animaux et les végétaux, *Soc. sc. méd.*, Lyon, 1882 ; *Biol.*, 1882 ; Nouveau mode d'administr. éther, chlorof., chloral à la sensitive ; application à la détermination de la vitesse des liquides dans les organes de cette plante, *C. R. Acad. sc.*, 1879 ; Influence des feuilles envisagées comme cause de la circulation des liquides nutritifs, *Soc. agricult.*, Lyon, 1883.—Cl. Bernard, Leçons sur les anesthésiques et l'asphyxie, Paris, 1875.—Budin et Coyne, Etat de la pupille, *Biol.*, 1875 ; *Arch. de phys.*—Dastre, Les anesthésiques, physiologie et applications chirurgicales, Paris, 1890 ; *Revue sc. méd.*, art. "Chloral," 1881.—R. Dubois. Anesthésie physiologique et ses applications, Paris, 1894.—Flourens, *C. R. Acad. sc.*,1851.—Joteyko et Stefanowska, Anesth. gén. et anesth. locale, *C. R. Acad. sc.*, 1889 ; *Biol.*, 1902.—Richet, Art.

"Anesthésie" dans *Dictionnaire*, index bibliographique.—Soulier, Traité de thérapeutique.—Vulpian, *C. R. Acad. sc.*, 1878.

Cocaïne.—Albertoni, Protoplasma, *Arch. ital. de biol.*, 1891.—Von Anrep, *Arch. de Pflüger*, 1880, p. 38.—Belmondo, Ecorce cérébrale, *Lo Sperimentale*, 1891.—Dastre, *Revue sc. méd.*, 1892.—Ferreira da Silva, Réaction . . ., *Journ. de pharm. et de chim.*, XII.—François-Franck, Techn. expér., *Arch. de phys.*, 1892.—Gley, *Biol.*, 1891.—Mosso, *Arch. ital. de biol.*, 1891.

Curare.—Cl. Bernard, Physiologie expérimentale ; subst. toxiq. et medic. : science expérimentale.—Bezold, *Arch. Reich. et du Bois-Reymond*, 1860.—Bochefontaine et Tiryakan, Conine . . ., *C. R. Acad. sc.*, 1878.—Boehm, Chemisch. Stud., *Beitrag. z. Phys. Carl Ludwig. Festschr.*, 1887 ; *Arch. de Pflüger*, 1875 et 1894 ; *Arch. de pharm.*, 1897.—Couty, Act. convulsiv., *C. R. Acad. sc.*, 1882.—Curare et strych., *Ibid.*, 1882.—Couty et Lacerda, Excit. muscul. du début . . ., *Biol.*, 1880 ; Le curare, son origine son action, ses usages, *Arch. de phys.*, 1880.—Dastre, Action du curare, *Biol.*, 1884.—Jolyet et Pelissard, *Biol.*, 1868.—Joteko, Curare et poisons curarisants, *Dict. de phys.*, index bibliogr.—Hermann, *Revue sc. méd.*, 1879, t. XIV.—Kölliker, *Arch. f. Anat. und Phys.*, 1856.—W. Mitchell, *Journ. de la phys.*, 1862.—A. Moreau, *C. R. Acad. sc.*, 1860.—Pélikan, *Bull. Acad. sc.*, Saint-Pétersbourg, 1857, t. III.—Pollitzer, *Journ. of Phys.*, 1886.—Schiff, *Ges. Beitr. z. Phys.* 1896.—Tarchanoff, *Arch.de phys.*, 1875.—Voisin et Liouville, *Journ. d'anat. et de physiol.*, 1867.—Vulpian, *Arch. de phys.*, 1876 ; Leçons sur les subst. toxiques.

Strychnine.—Cl. Bernard, Subst. toxiq. et medicamenteuses.—Couty, *C. R. Acad. sc.*, 1883.—Delaunoy, *C. R. Acad. sc.*, 1881.—Delezenne, Act. vaso-dilat., *Arch. de phys.*, 1894.—M. Doyon, Upas antiar, *Arch. de phys.*, 1882.—E. Heckel, *Revue scient.*, 1879.—Magendie, *C. R. Acad. sc.*, mémoire, 1809.—Martin-Magron et Buisson, Strych. et curare, *Journ. de Br.-Séq.*, t. II, III et IV.—Th. Mays, Brucine et strychnine, *Journ. of Phys.*, 1887.—A. Moreau, *Biol.*, 1865.—Ch. Richet, *C. R. Acad. sc.*, 1880, t. XCI, p. 131.—Schiff, Infl. pupille, *Arch. de Pflüger*, 1871.—Stannius, *Müller's Arch.*, 1837, p. 223.—Verworn, *Arch. f. Anat. und Phys.*, 1900.—Vulpian, *Arch. de phys.*, 1870 ; *C. R. Acad. sc.*, 1882, t. XCIV, p. 555 ; Leçons sur subst. toxiq. et médicament., Paris, O. Doin, 1882.

Atropine.—Heidenhain, *Arch. de Pflüger*, 1872.—Keuchel, Thèse Dorpat, 1868.—A. Marcacci, Cinchonamine . . ., *Arch. ital. de biol.*, 1888.—A. Meuriot, Thèse Paris, 1868 (bibliographie).—Nuel, Art. (Atropine) *Dict. de phys.*, index bibliogr.—Schmiedeberg, *Ber. d. Sach. Gesell. f. Wiss.*, 1870.—Schiff, *Moleschott's Unters.*, 1865.

Jaborandi.—Pilocarpine.—Gysi, Thèse Berne, 1879.—Hardy, *Revue sc. méd.*, t. XI, 1878, p. 767.—Langley, *Stud. fr. the Phys. Labor.*, Univers. Cambridge, 1877.—Ortille, *Bull. thérap.*, 1879.—Oulmont et Laurent, Hyosc. et datur., *Arch. phys.*, 1870.—Pilicier, Thèse Berne, 1875.—Pitois, Thèse Paris, 1879, No. 162.—Rabuteau, *Union médicale*, 1874.—Robillard, Thèse de Lille, 1881.—A. Robin, Étud. physiol. et thérap. sur jabor., Paris, Masson.—Vulpian, Leçons sur les subst. tox. et médicam.

Antagonism.—J.-N. Langley, *Brit. med. Journ.*, 1875 ; *Journ. of Anat. and Phys.*, 1880–1882.—Luchsinger, *Arch. de Pflüger*, 1877 et suiv.—Morat, *Revue scient.*, 1892 ; *Dict. de phys.*, art. "Antagonisme."—Is. Ott, Muscar. et atrop., *Journ. of Phys.*, 1878–1879.—Prévost, *Arch. de phys.*, 1877, et *C. R. Acad. sc.*—Rossbach, *Arch. de Pflüger*, 1875.—Sydney Ringer and Morshead, Atrop. piloc., *Journ. of Phys.*, 1879–1880.—Schmiedeberg, Elem. de pharmacodyn., trad. franc., 1893.—Sticker, *Centralbl. f. klin. Med.*, 1892.

Anæmia.—Cl. Bernard, Rapport sur la physiologie, 1867.—Richet, Les nerfs et les muscles.—Stefani et Cavazzani, *Arch. ital. de biol.*, 1888, t. X, p. 202.

PART II

Systematic Functions

The functions known as systematic differ from cellular functions as the whole differs from the part; they are the *functions which originate in the associations and definite relationships which are established between the cellular functions,* just as the systems which they sustain arise themselves from the associations and relationships effected between their component cells. These functions and these systems form, the first from the dynamic point of view, the second from the static, perfectly coherent aggregations; the animal organism itself is nothing more than an aggregation of this description whose nervous system helps to consolidate all the separate portions. By analysis this organism may be resolved into aggregations of the same nature, genuine partial systems, of which the surfaces of separation are continued into the nervous system in different directions. The definition of their frequently changing limits, their specific functions, their mutual relationships, is the end which it is the object of the study of the nervous system, regarded as a system, to attain; an end, in the present state of knowledge, still very imperfectly realized.

The conception of the system.—A system is a whole composed of parts having a determinate union amongst themselves which gives to the whole, that is to say to the system, its cohesion, its existence. A system is at the same time both a *unity and an aggregation:* it is one or the other, according to the tenour of the ideal or experimental analysis to which it is submitted.

In the universe nothing is isolated; every system is united to other systems by bonds external to itself; if these bonds with the exterior are broken, the system appears as a unity; if again, its internal ties be abolished, it is resolved into its component elements.

All the developments which follow each other in the nervous system show that this view is correct: the system contains bonds of union by which it is connected with the external world; on the other hand, its constituent parts are united together in such a way as to form a unity of which we are ourselves conscious.

The conception of an element.—Taken in an absolute sense, the word *element* signifies the irreducible limit to which analysis in a given science leads us. Regarded in a relative sense, it signifies some component part which analysis has isolated from a systematized whole. In an organized whole, such as the living being, the component parts which analysis demonstrates are themselves organized wholes, are systems in the real sense of the word, and these systems may be

themselves resolved into still more simple systems. Biologists frequently describe the elements as the component cells of the tissues. In spite of the fact that it is now understood that the cell is not an ultimate element, but that it is itself a system of microscopic dimensions, this term will be employed, because, in biological analysis, the cell expresses a limit far better characterized than any other; this is due to its boundaries being well defined and to its clearly being a unit.

Thus *the nervous system is composed of partial* or sub-systems, *more or less resembling it*, and analysis of these partial systems leads us, as in the case of other apparatus, to cellular elements. These elements have been studied in the first part of this work and now, being better known as regards their limits and constitution, are described as neurons. We have seen that, far from being homogeneous and incapable of subdivision, they present an internal organization and differentiated functions.

The conception of function. — In the living being all is function, because in it the whole tends to a determinate end. The idea of function is closely connected with and is superposed to that of system. Function represents the dynamic aspect of the living being, whose system represents the static aspect; it is nothing else than the bond of union which co-ordinates the several portions of a system and confers on it its unity.

Two kinds of function. — The study of the organism, that of its nervous system which reproduces its chief features, that of the partial systems into which it can be decomposed, shows that there are in it two kinds of bonds of union: some entirely internal, unite the different portions of the system so that its unity results; others, external, connect it with still larger aggregations, on which it depends and of which it forms part. Thus, from the very nature of things, there must always be two kinds of functions; the first, of a purely *internal* order, are called those of *conservation*, which in living beings may be generally described as functions of *nutrition;* the second are, on the contrary, functions of *external relation*, or of relation properly so called, of the organism or of the system under consideration with other organs and other systems of the same value.

External and internal relations.—It is perfectly obvious that the nervous system possesses these two orders of relationships and of functions. By it we are brought into relationship with our fellow-creatures, and it connects the component parts of our being by its internal bonds of union. But in proportion as we resolve it, by experiment, or merely by thought, into its component sub-systems of continually decreasing importance, the two orders of function become attributable to each of these units; each of these has its functions of conservation and of relation, and the same function is at once that of relation and that of conservation, according as to whether the organs which it unites are regarded as separate systems or as a coherent whole.

Plasticity of the nervous system.—And, as a matter of fact, these systems are susceptible of isolation and of fusion; thanks to the extreme plasticity of the nervous system, they approximate or separate according to extremely varied modes. Without absolutely breaking, the bonds of union relax at certain places while they become stronger at others. On account of this mobility and this gradation, the study of the functions of the systems is extremely difficult, but is none the less essential. In order to thoroughly understand it, it must be borne in mind that the phenomena of conscious sensation render necessary the association of a large number of co-ordinated elements; in other words, they are only developed in systematized assemblages of neurons. If, indeed, movement is everywhere present (whether visible or invisible) in cellular function, it is not the same as regards consciousness: *conscious functions are essentially systematic functions.*

PRIMARY DATA

Relations of sensation and of movement.—Whether functions express external or internal relations of the organism, that is to say, external or internal to a definite system, they are all based on fixed relations between those two phenomena which are known as movement and sensation. On the more or less complicated bond of union which exists between these two phenomena depends the importance of the function, and that of the system which brings it into being. In proportion as the organization becomes more complicated, that is to say, as the system becomes more closely united and superposed, the sensory phenomenon becomes more obvious and, in its turn, presides over more differentiated and more varied movements. This will be made clearly evident by analytical and detailed study of each one of the functions of the system. Only, in order to make this study more intelligible in proportion to the extent to which it is carried, it is necessary to recall some definitions and to clear up certain points concerning the two phenomena which are essential to the performance of every function of the living being.

The study of the function of innervation brings us face to face with two categories of facts which our present means of observation and of analysis are unable to further resolve: these are on the one hand *motion*, and on the other hand *sensation*. Not that this study does not enable us to recognize at every moment their relations and their dependences; but, doubtless, through the imperfection of the information which it supplies concerning both, it does not suffice to fill up the gap which separates them; hence it is necessary to accept the phenomenal duality which distinguishes them.

Origin of the two ideas.—The idea of movement comes to us primarily from the *exterior*. Our own special movements are only known to us as such artificially and by reasoning (reciprocal control of the different senses): as regards the inmost movements of our being, we can and shall attain a knowledge of them only by employment with ever-increasing assiduity of efforts of reasoning and of scientific analysis.

On the other hand, sensation is a fact *internal* to ourselves. The sensations of others, similar to those which we perceive in ourselves, are only known to us artificially and by reasoning (by comparison of the motor effects of these sensations in ourselves and in them); as regards the most elementary sensations of beings other than ourselves, they are and will be known to us only by continued efforts of reasoning and of scientific analysis; the method of study of the two phenomena, however contrary these phenomena may be, cannot differ fundamentally.

In short, we clearly perceive that external movement is continued in ourselves, and that sensation exists apart from ourselves; but we do not succeed in our efforts to superpose the two phenomena (neither in nor externally to ourselves) so precisely that the two may seem to us as being merely two points of view, two aspects, two varieties of one and the same thing, instead of being two distinct categories of phenomena incapable of resolution.

Analysis of the two phenomena.—In the present state of our knowledge, the study of movement is infinitely more advanced than is that of sensation. Hence movement serves not merely as a control, but also as a model for the study of sensation.

We know that complex movements are capable of resolution into simpler ones, and that this decomposition may be carried to a greater or lesser extent, without our being able to arrive at, in an absolutely certain manner, the first elements of movement. It is the same as regards sensation: there are complex sensations which surround elements capable of isolation, themselves more or less easily decomposable into still simpler elements. It is obvious at the first glance that

analysis may be carried much farther in the case of movement than in that of sensation. For a sensation to be presented to our consciousness, it is necessary that it arise in a nervous field developed in a very complex organization. On the contrary, if we endeavour to study synthetically the movements which correspond to it, especially in the nervous system, we shall be greatly hindered in our efforts.[1] Once more, the two orders of perception approximate one another, but the boundaries between them overlie one another, but are not superposed.

Process of association.—The most simple sensation of which we are conscious is thus, in itself, complex, and this complexity conceals a progressive series of operations in some degree based on the unity of the result. To adopt the more concrete language of anatomy, *sensation is not a cellular phenomenon, it is a systematic function.*—If sensation is real, it implies the association of elements which proceed from one of our senses to the cerebral cortex ; if it is a recalled sensation, a memory, it implies the co-operation of cerebral elements appertaining at least to the cortex, and perhaps to other portions of the brain, for in this case the limit is not easily determined. In any case it is a phenomenon of evolution, which implies a process of association as regards the cellular elements of the nervous system, or, more exactly, of the dynamic unities corresponding to their cellular unities.

Threshold of consciousness.—Consciousness has its degrees just as its field has also its variable limits. Every act which takes place in ourselves and of which we are not conscious may become conscious by the mechanism of the internal phenomenon which is known as attention. A moment ago, this act was below the threshold of consciousness ; then it has attained the level in which it becomes clearly conscious. This threshold corresponds therefore to a degree of consciousness somewhat arbitrarily fixed, in order to eliminate from the consciousness everything which has only a doubtful value or is perceptible with difficulty. Practically, we relegate to the unconscious all bare consciousness of the being, and we retain the name *conscious* for the recognition, more or less analytical and detailed, of the being.

Simple sensation.—If sensation presents degrees and shades in its intensity, it presents yet more of these in its complexity. We accept, as we have said, as elementary a fact which we know is fundamentally complex, but which resists that internal analysis to which we endeavour to subject it in ourselves. This fact is what is known as *simple sensation.* The prick of a needle, the sight of a luminous point, the hearing of a short sound, supply us with ordinary examples of it. Simple sensation is yet accompanied with perception ; the object is perceived as being such in its own character ; that is to say, it is recognized. If perception is wanting, there is merely *crude sensation.*

Specific modalities.—These different examples of sensation, touch, light, sound, etc., represent what is known as specific varieties (incapable of reduction the one into the other) of sensation ; further, each one of them may include various gradations (colour, tonality, etc.).

Complex sensations.—Simple sensations of varying gradations combine among themselves to form complex sensations, in which the component elements are so fused together as no longer to appear distinct from one another ; every sense furnishes examples of this nature. The specific sensations of the different senses are combined, in their turn, to form a phenomenon which no longer bears the

[1] If this should cause surprise, it must be remembered that our organism is constructed for a practical and not for a speculative end. Sensations which should be localized in areas which should correspond to our component cells would be, by their excessive accuracy of localization, useless to us ; just as direct synthetic vision of movements which correspond to an ordinary sensation would distract us from the consideration of much more simple external movements, which it is important for us, on the contrary, to be acquainted with.

name of *sensation* and which marks definite progress in the evolution of this series of internal phenomena.

Idea.—By their association, these sensations, whose form, source and complexity are so different, give origin in their turn to a new psychical process still more complex than themselves; this is *ideation*. The origin of sensation, starting from these elements, is unknown to us as regards its mechanism, because they themselves are not accessible to consciousness: in other words, consciousness only becomes clear in proportion as these elements are associated in a sensation: when isolated, they elude it. The genesis of ideation, by the association of sensations, becomes on the other hand accessible to *internal observation*. Psychology has always extensively employed this method, in order to study the formation of ideas. At the present time progress in this direction has been made by causing *external observation* and *experiment* to be made use of in this study. In man and animals lesions of the nervous system either exist or are induced experimentally, by which these complex manifestations of consciousness are disconnected, the one being suppressed, the others being allowed to continue; and thus we gain an insight, although a feeble, and too often uncertain one, concerning the conditions of their existence.

Cognition; Recognition.—The psychical elements which form sensations and ideas are not merely associated in an actual and contemporaneous fashion, but also the regular functional activity of the nervous system further provides them with a bond, an association, originating therefore a continuity in time. New ideas and sensations which arise in us recall the existence of sensations and of anterior ideas of the same order; we recognize the objects, movements, phenomena, symbols which have already made an impression upon us, when this impression is renewed. This recall of sensations and of previous ideas, which seemed to be effaced, implies that they were in reality preserved in a latent dissimulated condition, which is called, specifically, the *unconscious state*. New impressions bring them back to the threshold of consciousness. This is the remembrance or recognition of phenomena with which we have already been in touch.

Residue.—In other words, every impression, every sensation leaves a *residue* in us. New sensations of the same order are added to it, consequently are associated in it, by recalling it to actuality. This identification of the new phenomenon with the old through time permits us to recognize it; were this identification wanting, there would be for us no experience of the past, the action of the external world on our senses would be continually a new one, that is to say, one perpetually unknown.

Remark.—It may seem that these data on psychical processes would be more appropriately placed at the end of the study of the nervous functions, as being its finishing point, and not at its commencement. We shall meet with them again in the analysis of a certain number of special cases, particularly the function of language; but from the very first steps which we shall take in this study, it is precisely these phenomena of sensation that we meet with, occurring as they do as the inevitable consequence of every investigation, of every analysis of the nervous system. In the study of movement we may, if we wish, proceed from the simple to the compound; in the order of sensation, an already synthetized phenomenon is offered us, as the first discernible datum. Hence we are compelled to describe it summarily at first, at the risk of being forced to justify our affirmations, in proportion as the facts resulting from observation and experiment shall be displayed before us. Less than any other science can psychology proceed by deduction; in the living being everything is allied, everything is closely connected; hence it results that, in the study of its functions, we must proceed from the complex to the simple in many cases.

FIRST SECTION

NERVOUS ORGANIZATION

At the foundation of nervous organization lies a bond of union, a reciprocal dependence between sensation and motion. Its perfection is obtained through multiple and graduated forms which affect both phenomena, as also from the numberless associations which they are capable of effecting. The centripetal paths convey impulses which are from their origin both multiple and diverse (sense organs); the centrifugal routes terminate in muscles (or equivalent organs), themselves both numerous and diverse, for the performance of visible or concealed acts, which indicate the end of the evolution of the nervous process. From the commencement to the end of the latter sensory phenomena are interpolated; its value increases with the complication of the nervous paths, followed by the impulse, and also by the length of time which it occupies in these paths.

This complication is based on a regular system; it proceeds on simple lines and on a plan, the object of which can be recognized. First of all it is necessary to describe this general plan, by which the organization of impulses is rendered intelligible. By adding to it the data furnished by experiment, we shall be able to observe the progress of these latter, their results now divergent, now parallel, and again divergent; their numerous conflicts; their reinforcements; their divisions and their postponements: all the circumstances which do not explain to us these results of internal observation which we describe as sensation and ideation, yet which manifestly give rise to them and give us command of them in experimental practice, and, nowadays, in the treatment of nervous diseases.

Its scheme.—Anatomically a distinction is made between a *peripheral* nervous system and a *deep* nervous system (the latter being generally known as *central*).

(a) *Inferior system.*—This distinction is justified physiologically on the condition of a division being made, not at the termination and at the apparent origin of the sensory and motor roots, but at their real termination and origin in the grey substance of the medulla oblongata and spinal cord. The conventional limit of the two systems is defined in this grey matter.

The long cylinder which the latter forms is the *direct* rendezvous of peripheral

impressions, and is at the same time the point of *immediate* departure of the motor reactions ; it is a spot in which the impulses are systematized and organized ; it is the keystone of the *peripheral* or *inferior* system.

(b) *Superior system.*—Another locality, in which grey matter, assuming the form of a folded sphere, is found, is the surface of the brain, and is united to the preceding by connexions in which the conduction is, on the one hand, ascending and on the other descending, by which impulses are conveyed to it and by which they are carried from it. It has no communication with the exterior except in an *indirect and mediate* manner ; it works on the materials prepared by the grey axis, to which it gives a new organization, and it reacts on the exterior by the intermediation of this same grey axis, whose motor associations, also ready prepared, it makes use of : it is the keystone of the deep or *superior* system.

The conductors which carry the impulse (in two different directions) between the periphery and the grey axis are the so-called *fibres of projection of the first order.* Those which convey it between the two areas, previously pointed out, of the grey matter are *fibres of projection of the second order.*

Extension of the grey axis beyond the spinal column.—Ganglia of the great sympathetic.—This very simple scheme requires some corrections and additions in order to accurately represent the real condition. Externally to the spinal canal, the grey axis is prolonged in the form of small grey disseminated masses, the *ganglia of the great sympathetic,* which possess the sensori-motor functions of the spinal cord.

Superior prolongations of the grey axis.—High up, above the medulla oblongata, the grey axis, after it has gathered together all the conductors of general sensation, is surmounted by discontinuous masses (the internal and external *geniculate bodies, the corpora quadrigemina,* anterior and posterior, *the mammillary bodies*), which appertain to the special senses (hearing, vision, smell) and form, from a functional point of view, differentiated prolongations of this same axis. Still higher occurs an important grey mass, the *optic thalamus,* which introduces a new complication into this edifice, hitherto apparently so simple. This mass, composed of distinct areas, of which each belongs to one of the modes of sensation which are diffused through the nervous system, is no longer placed at the union of the fibres of projection of the first and second order, but in the very course of these latter. To express the matter more clearly, the ascending or sensory fibres, which proceed from the grey axis to the cerebral cortex, are interrupted in the optic thalamus, the larger proportion of them as regards the majority of observers, entirely for others. This very obvious interruption is not the only one which the paths of ascending impulses undergo ; similar interruptions are found from the spinal cord, so that these paths are divided into two species : the one *long,* proceeding from the grey axis to the cortex, the other *short,* whose length varies according to circumstances.

Another organ, which must also be regarded as possessing the importance of a system, is the cerebellum, which, through the connexions uniting it to the grey axis and to the cortex, complicates yet more this assemblage, which is known, in its totality, as the superior or deep system. In every case, the course of the impulses which traverse this superior system is extremely varied and, from this point of view, contrasts with the relative simplicity of their progress in the inferior system.

Equivalent juxtaposed systems.—In addition to the divsions which have just been pointed out, the nervous system possesses yet others in a quite different direction. In addition to the transverse incisions marking its stages, it displays fissures on its length which also have the value of differentiated systems. At its origin in the organs of sense, the nervous system affects territories as well as functions which are distinctly separated ; at the surface of the brain, the cortex (a

remarkable fact) reproduces these divisions. It reproduces them by repeating, not merely the areas devoted to each sense, but certain topographical divisions and subdivisions of these territories themselves. The brain is metamerised like the spinal cord, the word *metamerised* being used, it is true, in its most general and not in its strictly embryological meaning. The optic thalamus offers a similar metamerisation, repeating that of the sensory, peripheral, medullary and, lastly, cortical sensory territories. The cerebellum, the least metamerised of these grey masses, has more special connexions with some senses than with others (equilibrium, sight, touch).

Association of the systems.—Such is the plan, once again very simple, which divides the nervous system into systems, no longer superposed, but juxtaposed, which receive from the preceding ones their constituent elements. But once again, also, it must be repeated that these are merely the chief constructive outlines. They support others, which ensure the multiple connexions between these equivalent but specifically differentiated systems, which they render more obvious to us. From the spinal cord, the impulses coming from the periphery are co-ordinated by associations effected in the grey matter of the cord, and the impulses which, from the spinal cord are forwarded to the muscles, are in the same way organized by it. Of the original metamerisation of the spinal cord, but little remains in the case of the superior mammals, and above all in man, at the period of their complete development. The segments of the grey axis are fused into more and more numerous functional associations, and special conditions must be present in order that the isolated function of these segments may be recognized. The optic thalamus presents connexions of the same kind, but still more marked. This mass of grey substance no longer collects merely the impressions arising from a single source, like the spinal cord, the *geniculate bodies* and the *corpora quadrigemina*, but all those proceeding from all the senses which are represented in it and which are in a certain measure organized therein. This great ganglion is qualified for the reflection of these impressions, when transformed, upon the organs of motion ; an essential rôle is attributed to it as regards *instinctive and emotional manifestations.*

In man the most powerful organ of association is the brain. The sensorial systems, which terminate in its cortex, find in it and in the tangential fibres immediately subjacent to it those internal connexions which organize them. These same systems find in the commissures of varying lengths and direction which furrow the cerebral mass, the links which, in their turn, fuse them into a common functional activity.

Functional localizations.—The nervous system is composed of unities, of elements, which, from the first to the last, have a differentiated function and one in a certain sense specific. But this differentiation is generally progressive and graduated, and resides principally in the connexion of these elements amongst themselves. For convenience of study, we sometimes voluntarily neglect these graduations, in order to collect together the objects and the phenomena under a common type ; again, on the contrary, we give them undue importance in order to mark, in the two cases, that distinction which is appropriate between them ; for, otherwise, the infinite detail would lead to confusion. Hence have arisen the discussions between those who would localize and those who would not localize nervous functions, discussions arising much more from the exaggeration of the individual point of view than from absolute error.

Three points of view.—In order to render these discussions intelligible, it is necessary to clearly understand the nature of system and of function, such as has been pointed out above. As regards the nervous system, three points of view which should be separated have often been confounded. These three points

of view regard, the first the *succession* of phenomena, the second their *equivalence*, the third their *gradation* ; hence arise three orders of localization which have not always been properly distinguished.

(*a*) The several portions of the nervous system transmit activity in a definite direction. In this evolution sensation first appears, then the apparent movement by which functions are exercised ; hence we recognize in the nervous system a sensory portion and a motor portion successively arranged.

(*b*) In the nervous system sensation and motion manifest different modalities which are developed in parallel and equivalent systems. The idea of localization corresponds above all to the distinction of these systems as ordinarily understood, that is to say, in so far as these systems become flush with the cerebral cortex at their superior terminations.

(*c*) Lastly, whatever may be the order of sensation which governs the motor act (whatever may be the sensorial organ which furnishes the impressions) this sensation manifests degrees according to the more or less deep routes in which the impulses received in the organs of sense travel : in other words, according to the height at which the impulses are reflected : whence the division of acts into new categories of unequal value, of which the three principal are, from this point of view, called *automatic* (reflection in the spinal cord), *instinctive* (reflection in the optic thalamus), *voluntary* (reflection in the cerebral cortex). Consciousness has its degrees, which are determined by the more or less complex organization of impulses.

Restriction.—None of these indications must be taken in an absolute sense ; not one of the phenomena to which they relate is an isolated one ; none of the systems which support them is absolutely independent ; all mutually influence each other.

Every time that some part of the nervous system is stimulated or suppressed there is at all events a temporary reaction of this modification on the whole system. This reaction is immediate or remote, and, in the latter case, is often so weak as to be inappreciable. The perturbation thus induced varies according to the part of the nervous system which has been modified. Hence the inference may reasonably be drawn that the portions experimented upon possess different functions. But the argument is often carried still farther, the function being localized in the region experimentally modified, which has been the point of departure of the observed disorder, and in doing this it is clear that the teachings of experiment are overstepped. The nervous system is composed of parts which are at the same time both conjoint and functionally differentiated.

CHAPTER I

SENSATION AND MOTION—THEIR RELATIONSHIPS

The *ego* in itself only perceives sensations, outside itself it only perceives movements. The movements of our own limbs would be for it merely those of foreign bodies were it not for the sensations which attach them to it and, indeed, they become such with regard to the *ego* when they are no longer sensitive. How does our *ego* recognize the existence of sensation in the case of beings other than ourselves ? By a process of reasoning founded on analogy, and not otherwise.

Analogical proof.—If I wound an animal and it begins to struggle and cry, I say, without any doubt, that it feels ; seeing that it manifests the same reactions as those by which I express my own sensibility, I affirm that it also possesses the same, and I am able to estimate the quality and the amount of the sensation. Between it and myself, as between myself and it, there is merely movement ; but in myself there is a definite link between sensation and movement, and this enables me to recognize sensation by means of movement, and by this indirect means to estimate it as a fact accessible both to observation and experiment.

Law of continuity.—The more closely the motor reactions of the being are assimilated to mine, the greater I presume to be the resemblance of its power of sensation with my own. In proportion as this resemblance gives place to a more remote analogy, so does the amount of sensation which it represents become less and farther removed from that which is personal to myself. If, however, this degradation follows a regular progression, I shall then be in a position to connect the fact of this transformation and diminution with my power of sensation, which is the only criterion available to me for estimating facts of this nature. It is the same with sensation as with life, which it characterizes : we see its field continually increasing, without our being able to precisely define its limits ; and this increase is effected, at each new stage, by the adjunction of beings of a nature at the same time inferior and analogous to that of beings previously considered as being of the most elementary structure.

Anthropomorphic reasoning.—Except for the infinitesimal part which each one of us plays therein, a knowledge of the living world is based on anthropomorphic reasoning, and it is impossible to base it on any other reasoning.

Hence it is necessary to exert great prudence in employing it.

A. THE ROOTS OF THE NERVOUS SYSTEM—THEIR FUNCTIONS

The bond of union between sensation and motion is, in a living being, an obvious fact.

We can destroy this bond ; we can cause movement and sensation

to reappear, isolated one from the other, by making use of different portions of the nervous system.

I. The Simple Facts ; General Laws

1. **Nerve pairs.**—The nervous system with its superior termination, the brain ; its fundamental portion, the spinal cord ; and its peripheral distribution, the nerves, being regarded as a whole, it will be noticed that these last are inserted along the whole length of the cord on each side by two roots, one *dorsal* (posterior in man, superior in animals), the other *ventral* (anterior in man, inferior in animals). These are indeed the roots of the nervous system, that is to say, the paths by which the relations of this system between it and the external world and with the exterior are established, and this in a double direction, and conversely. Thus symmetrically arranged, they form nerve pairs, one on each side, corresponding to each of the metameric divisions of the spinal cord.

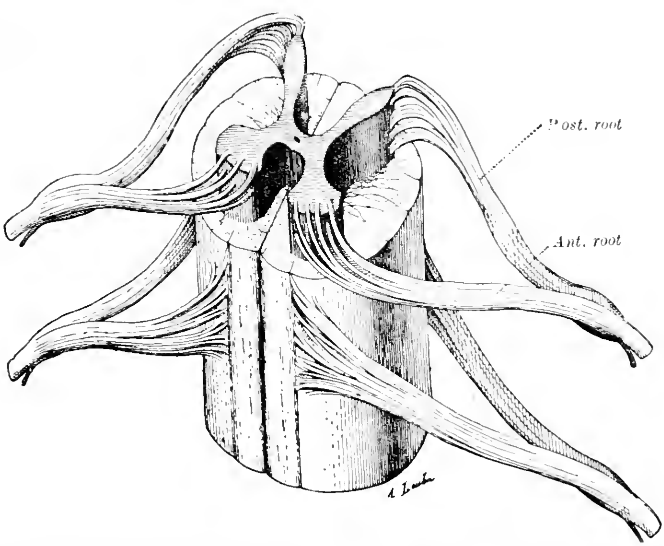


FIG. 49.—Two nerve pairs at their origin in the spinal cord. Anterior and posterior roots.

As regards the upper pair, the figure shows the relations of the roots with the grey axis and the fluted shape of the latter. In the lower pair is seen the emergence of the anterior roots at the surface of the spinal cord, and in the anterior collateral furrows.

Distinct functions.—For a very long time it was supposed that these roots had different functions, and hypotheses were elaborated with the object of pointing out the nature of these functions.

To Ch. Bell (1811) belongs the merit of invoking the aid of experiment in order to solve this problem ; but, operating on animals at the very

moment in which they were killed (rabbits killed by distension of the medulla oblongata), he was not able to determine the function of the posterior roots, which he considered to be devoid of sensation, and he merely detected the motor excitability of the anterior roots, which he considered, further, to be sensitive.

In order to understand the experiment of Ch. Bell and the signification which he attached to it, it is necessary to be cognisant of his point of view. Imbued with the then current ideas of Willis concerning the nervous system, he endeavoured to verify the latter. Willis regarded the brain as the centre of sensation and of movement, while the cerebellum presided over vital actions (circulation), nutrition, secretion, etc.). Guided by anatomical results, Charles Bell described the anterior roots as being conducting paths in direct continuation with the brain through the intermediation of the crura cerebri, and the posterior roots as tracts directly connected with the cerebrum by the intermediation of the restiform bodies (it is now known that in reality the connexion is far less simple). The anterior roots would thus represent the functions of the brain (sensation and movement); the posterior roots those of the cerebellum (phenomena of nutrition).

Experiment, as performed by Charles Bell, does not verify all these assumptions: it only confirms one of them, the motor function of the anterior roots, but remains mute as regards all the others. On this account, indeed, it did not appear to him contrary to the hypothesis which served as his point of departure; in any case, it seemed to him sufficient to support the doctrine of Willis, which it was his object to verify. Apart from any hypothesis, however, the experiment of Charles Bell established a fact new for his epoch, namely, that the anterior root manifests functions which are not displayed by the posterior root; in other words, that there is a functional difference between the one and the other root. As to the nature of this difference, it wholly escaped him. It did not become clearly comprehensible (for him, as for every one else) until some years later, after the researches of Magendie on this subject.

Nature of these functions.—To A. Magendie incontestably belongs the merit of having ascertained the truth on this point through his decisive experiments (1821).[1]

Experiment.—The experiment is easily made on the dog, and preferably on a young animal (softness of the bones, length of the roots and the special arrangement of the dura mater, which directly invests the spinal cord). The animal is anæsthetized and is kept insensible during all the preliminary operations.

It is only permitted to recover consciousness at the time when the

[1] In France, as also abroad, the discovery of the separate functions of the nerve roots is generally attributed to Charles Bell. As a matter of fact, he misconstrued them, and they were exactly formulated for the first time by Magendie, by means of the very apt experiments which he employed to demonstrate them. This has been recognized and maintained by all the authors who have studied this question of priority. (Consult Cl. Bernard, *De la physiologie générale*, pp. 15 and 216.—Vulpian, *Leçons sur la physiologie générale du systéme nerveux*, p. 109 et suiv.—Chauveau, *Journal de l'anatomie et de la physiologie*.—A. Waller, *Éléments de physiologie humaine*, p. 596.)

roots are acted upon. A limited region being taken for investigation, as that of the posterior limbs, the roots of the nerves which correspond to them in the lumbo-sacral region of the spinal cord are laid bare. For example, all the so-called posterior roots (superior in the animal) are cut on the right, and on the left all the so-called anterior roots (inferior in the animal).

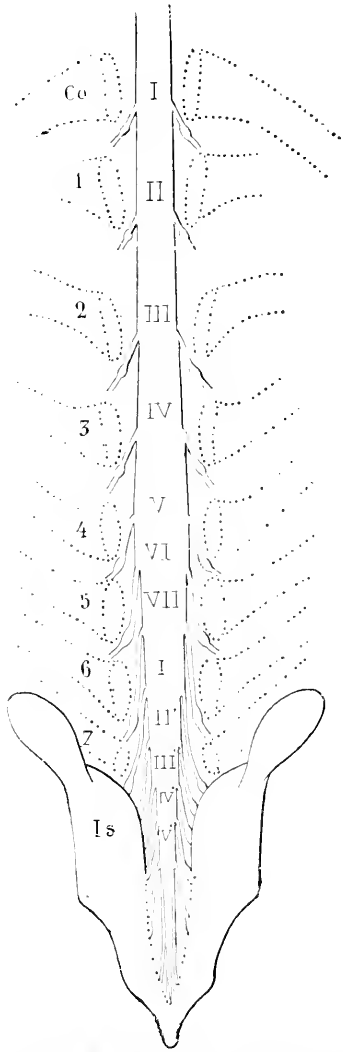


Fig. 50.—Medullary roots of the lumbar and sacral regions in the dog.

The diagram shows the point of emergence of each of the roots from the spinal cord in relation to its exit from the intervertebral foramen. Obliquity and relative length of the sixth and seventh lumbars and the first sacral.

Co, last rib. 1 to 7, transverse apophyses of the lumbar vertebræ, of which the posterior arch is removed. *Is*, illiac bone.

(a) *Effects of the section of the roots.*—As a result of these sections, the limb on the right side continues to move, but *ceases to be sensitive ;* it may be pricked, pressed or burnt without provoking reactions on the part of the animal. The limb on the left side continues to be sensitive, *but ceases to move ;* the animal is incapable of using it for walking or for any other purpose.

Hence it follows that *the posterior root is sensory*, that is to say is connected with the exercise of sensation ; *the anterior root is motor*, that is to say, connected with the performance of movement.

(b) *Effects of stimulation.* — By cutting the posterior and anterior roots we have not destroyed or suppressed the organs of sensation and of movement, but we have interrupted the paths by which the impulse which arouses the first or excites the second is conveyed. Indeed, *if the central end of a posterior root* is irritated, the animal reacts, that is to say, *feels ; if the peripheral end of an anterior root is irritated*, the corresponding limb is *moved*.

If, conversely, the peripheral end of a posterior root is irritated, or the central end of an anterior root, no reaction of such a nature as

those which have just been referred to, either sensory or motor, results. By this second test a new conception, and a very important one, is added to that of separation or distinction between sensation and movement ; that, namely, of direction, of orientation, or of *polarization*, as it is generally termed.

LAWS OF MAGENDIE.—1. **The posterior or dorsal root conducts impulses from the periphery to the central portions of the nervous system, to the special organs of sensation ; it is sensory.**

2. **The anterior or ventral root conducts impulses from the central portions to the periphery, to the special organs of movement ; it is motor.**

Dynamic polarity.—The dynamic polarity of the neurons has no other experimental foundation than this. We now say of the neurons that which it has been customary, since the time of Magendie, to say of sensory and motor fibres, namely, that some conduct in one direction and others in the other, which presupposes two poles for each. It is true that anatomy has enabled us to observe the exact situation of those of these poles which are located in the grey matter, and this is an incontestable advance ; but the idea of direction has been supplied by physiology, and can be furnished in no other way.

2. **Current of entry, current of exit.** — Hence, in the altogether similar fibres of these two parallel nerve trunks (posterior and anterior root) impulses circulate, of which some represent *a current which enters the nervous system* and others *a current which leaves it.* The more special nervous phenomena (psychical phenomena or those of sensation) manifest themselves in the interval ; that is to say, in the complicated network which the elements of the spinal cord and brain form between them. Visible movement is external, in the muscles or analogous organs.

Order of succession of the two phenomena, sensory and motor. — In the nervous process regarded as a whole, movement ensues after sensation, of which it is the visible consequence. This general current of cyclic form, which commences in the organs of sense and finishes in the muscles, is never inverted. *In the nervous system,* as in the vascular system, *circulation is effected in a definite direction.* Temporary checks may occur, or different routes may be followed, but it never returns on itself.

Abbreviated image of the whole cycle.—If it is desired to observe this cyclic process in its totality, it is only necessary to repeat the experiment in different conditions : between the posterior and the anterior root only the corresponding segment of spinal cord is left, by cutting the latter above the lumbar region, in such a manner as only to permit *reflex* action. When limited in this way, the complexity of the phenomenon disappears, and only the most obvious details are

observed ; but, on the other hand, it is possible to ascertain the direction which it follows in the nervous system.

Comparative Physiology.—Batrachia.—Fodera and J. Müller, have extended the discovery of Magendie to cold-blooded animals. The frog, on account of the shortness of its spinal cord and the relative length of its lumbar roots, is one of the animals best adapted for every kind of experiment on the nerve roots.

Birds.—The fact has been verified as regards birds by Schiff, and more especially by A. Moreau.

Fishes. — A. Moreau has also proved it as regards fishes, making use of the ray, the torpedo, etc., species in which the roots, after their reunion in the ganglion, remain easily separable for a certain length before forming a mixed nerve.

Invertebrata.—It has been endeavoured to ascertain if the invertebrata present an analogous dissociation of the nerves of sensation and of movement at the spot where the peripheral nerves leave the ganglionic chain, which in them represents the spinal cord.

Newport, Longet, Faivre, Vulpian have endeavoured to ascertain this, the first by dissections, the others by cutting experiments and excitation of these nerves laid bare in animals such as the lobster, crayfish, etc. It has not been possible to demonstrate that in these animals the sensory and motor elements are grouped in distinct bundles, as in the vertebrata. According to Vulpian, the elements of the two orders must be mixed, inasmuch as all the nerves which may simulate roots give rise to manifestations both of sensation and of movement.

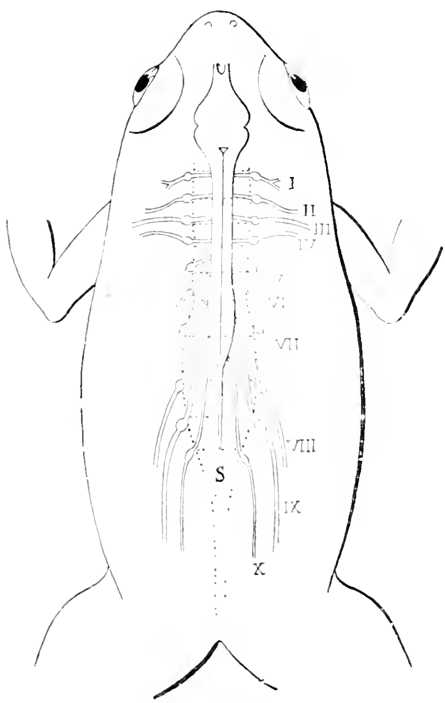


FIG. 51.—Diagram representing the medullary roots in the frog.

S, sacrum represented in dots. Above it and also in dots are shown the limits of the vertebræ between which the nerve pairs find an egress by the intervertebral foramen, after a more or less oblique course. The spinal cord is much shorter than the vertebral canal which terminates at the base of the sacrum.

I to X, spinal nerve pairs, whose posterior root and ganglion may be observed in the spinal canal, and the mixed trunk outside it.

No absolute distinction between sensation and motion.—The experiment of Magendie therefore shows, in a very clear manner, the distinction between sensation and motion. But how must it be interpreted ? Is it to be assumed that there is an absolute localization within definite boundaries ; or rather, the two phenomena being everywhere closely associated, is it merely that there is an exaggeration of one or of the other in special organs ? This last is the true interpretation.

Motion concealed under the sensory phenomenon.—And first of all, as concerns sensation, it is only in an abstract manner that we can regard it apart from movement. Not only, indeed, does it take origin from a movement (exciting impulse on the posterior roots), but, throughout its development in the deep masses of the nervous system, it is accompanied by a movement, invisible, molecular, but not the less real. The importance of this movement does not consist in its quantity, which is infinitesimal, but in its complexity, which is extreme ; it is the co-ordination and the synthesis of its component elements which give it its unity. And it is this which makes it absurd to seek for the mechanical equivalent of sensation. Thus, in stimulation of the posterior root, the phenomenon of sensation is so evident, so marked, that it arrests our whole attention ; but it must not prevent us from recognizing the phenomenon of motion, on which it is superposed, and which indeed presides over it.

Sensation disguised under the motor phenomenon.—Conversely when movement is induced in the muscles through excitation of the anterior root, every trace of sensation seems to be absent in this organ and in the motor nerve ; yet both are composed of excitable elements, that is to say, of elements possessing the earliest germ of sensibility ; so that here also, under a more marked phenomenon, this time motion, we must suspect another, latent and concealed, which is in this case sensation. Both phenomena are present in every living portion of the body. But that which makes sensation evident is obviously organization, the synthesis of living elements into a co-ordinated system. That which degrades sensation and reduces it to its simplest expression is the dislocation of the system, its reduction to its simple elements in which movement alone seems to be present, as in non-organized matter.

This is the reason why the stimulation of the two roots of the nervous system (anterior and posterior root) has such different effects. Individually considered, they have the same mutual value as any other tract of the brain or spinal cord, but one is at the entrance to the system, and its stimulation extended over the whole of this system will elicit the most remarkable of its manifestations ; the other is at its exit and, as such, can only manifest the properties of the isolated element which it governs : the one takes part in a *synthetic*, the other in an *analytic* phenomenon.

3. **Functional bonds of union.**—The nerve roots display distinct functions, but these functions are not independent. The connexion which exists between sensation and motion is manifest, so far as it has been investigated, in all the experiments made on these roots.

Influence of the posterior roots on the excitability of the anterior roots.—Harless, Cyon, Dastre and Marcacci have observed that, after section of a posterior root, the excitability of the corresponding anterior root (by an induced current) is modified. The first of these authors has observed it to be diminished, the others, on the contrary, to be increased. Belmondo and Oddi, investigating the cause of these variations, think that it lies in the fact that the section of the posterior root acted for a certain time as a more or less persisting irritation, before suppressing the propagation of the impulses which are transmitted by it as they come from the periphery. In order to overcome the irritating action of mechanical section, they cocainized the root in which they wished to suppress this phenomenon, and they then found that the excitability of the anterior root is always lowered after its physiological interruption.

According to these facts, it would appear that, in addition to more or less lively *accidental* stimulations which are furnished it, the posterior root is the seat of a sort of slight but *constant* flow of impulses, which proceed to the spinal cord and thence to the motor roots. When the diastaltic system is not interrupted in any point of its course and the anterior root is stimulated in its course, this impulse is added to those which are already circulating in it, and the effect of it is then greater, if, the posterior root being cut, this circulation should be from this fact interrupted. Hence the sensory nerve is in a constant state of tonic stimulation, a condition similar to that which is known to exist in the muscle, and of which it is the exciting cause. When a strong excitation arises, and visible movement is produced, this tension is exaggerated ; when every route available to the impulse is cut, this same tension disappears, and the tone is said to cease. The source of tone is, in fact, this permanent current of impulses, the latter being slight and imperceptible.

Influence of the posterior roots on motor functions.—When only a posterior root is cut, its suppression does not act in a very obvious manner on the motor power of the corresponding anterior root. This is so because the grey matter of the spinal cord is a locality in which a large number of other impulses converge, both those coming from the uncut posterior roots, and those which have been stored up in the superior parts of the nervous system, and which easily supplement the deficit due to such a limited lesion. But if a certain number of sensory roots be cut, for example, all those which correspond to the posterior extremity, it is seen that the movements of this limb, without being abolished, are curiously disturbed. Cl. Bernard, Chauveau, Tissot and Contejean, who have performed this experiment, point out the inco-

ordination of the movements which is the consequence of it. In persons suffering from locomotor ataxy a lesion of this nature, affecting the inter-medullary prolongations of the posterior roots, gives rise to that inco-ordination of movement which is so obvious in their mode of progression. And it has been proved that there is an entirely sensory form of locomotor ataxy, which is the result of an alteration of the sensory nerves (polyneuritis), apart from any affection of the spinal cord.

2. **Organic Complications; Recurrent Sensibility.**

The very obvious distinction which exists between the nerves of sensation and of motion, in the posterior roots, presents, nevertheless, a paradox, which for a long time compromised the law so clearly enunciated by Magendie concerning the functions of these roots, and this obscurity existed until a rational explanation of this paradox was given.

1. **The fact and its conditions.**—The roots being laid bare, if, before cutting them the posterior root be pinched, it is found to be very sensitive; but *if the anterior root be pinched it will be found to be equally sensitive.* The fact was in the first instance observed by Magendie, was successively accepted and denied by Longet (1840–1841), then re-discovered by Cl. Bernard, who propounded the conditions which give rise to it. In order the better to observe it, it is necessary to wait until the animal shall have recovered from the operative shock by a sufficiently long repose. The logical solution of the paradox is due to Longet. The sensory elements contained in the anterior root do not arise from the origins of this root, but are nothing else but elements of the posterior root, which, instead of going to the skin, re-ascend into the anterior root by a re-current course, in order to confer sensation on the membranes which envelop the spinal cord.

Analysis of the phenomenon.—*If, indeed, the anterior root be cut and the two ends be investigated, the inferior will be found to be sensory* (as also motor) and not the superior, irritation of which gives rise to no kind of result. *If the corresponding posterior root be cut, all sensation disappears from the anterior root,* whether cut or not. Sensation in the anterior root is, then, clearly a borrowed sensation; the anterior root is only a place of passage for sensory fibres which go to the membranes either of the cord, or of these roots themselves. Hence the paradox is explained; *so-called recurrent sensibility is nothing more than a special case of general sensation.* The apparent exception to Magendie's law is included in this same rule and fully confirms it.

Anatomical proof.—If, in reality, sensory fibres which have their trophic centres in the cells of the vertebral ganglion, enter by recurrence into the anterior root, it is possible to make them evident by the method of Wallerian degeneration. By cutting the anterior root, these fibres are cut at the same time as those incomparably more numerous fibres (motor fibres) which have their trophic cells in the anterior cornua of the spinal cord. Both will degenerate, but in opposite directions, some in one of the two ends of the cut root, the rest in the other, and they will in this way be recognizable, the degenerated fibres surrounded by healthy ones, the healthy ones by degenerated. And this, as a matter of fact, is what happens: the medullary end of the anterior root which has been cut contains some degenerated fibres amongst its healthy ones, and the peripheral end some healthy fibres among the mass of degenerated motor fibres. The fibres which are present in small number, and which have an orientation contrary to the others, are clearly the sensory recurrent fibres. This experiment was first made by Schiff on the roots (1850). Philippeaux and Vulpian have repeated it on the hypoglossal and facial nerves.

Arloing and Tripier also made use of this method of control when they investigated the question of recurrent sensibility under a new aspect.

2. **The reason.**—It is surprising at the first glance that sensory elements should be present in membranes such as those which cover the spinal cord or the coverings of the nerve trunks; because, as a matter of fact, these membranes are generally found to be insensitive when experimented upon, and in theory, the only membranes which would seem to require sensibility are those which face the exterior, such as the skin or the mucous membrane.

But *sensation* is not necessary for us only in our relations with the external world, it is *indispensable as regards the relationship of all our organs to one another*, of all our cells between themselves; it is the great regulator of function. Only this sensation is not conscious in the personal sense of the word; and yet it may become so as the result of changes due to traumatism, in the deep portions of the organism. This is one of the reasons which cause it to appear (by rendering it obscurely conscious or sub-conscious) in the dura mater and the roots a certain time after the opening of the spinal column after the animal has had time to recover the shock of the first operation.

As regards the cranial dura mater, it has been found that filaments are given off by the trigeminal nerve, and this membrane was known to be sensitive by former observers. It possesses great numbers of nerve fibres, and these latter are furnished with receptive apparatus analogous to those of touch or of general sensation.

Site of the recurrence.—The recurrence of the fibres which, from the posterior become involved in the anterior root, is not carried out at the union of the two roots, in the mixed trunk which is the result of this union; it is effected much farther away, in the plexus which arises from the combination of these trunks. Section of the mixed

trunk in the neighbourhood of the roots abolishes sensation in the anterior root, just as if the posterior root had itself been cut (Cl. Bernard).

Cl. Bernard maintains that every anterior root acquires its recurrent sensibility from the corresponding posterior root, and not from another. According to him, this correspondence would be one of the characteristics of the physiological nerve pair; he employs it more particularly in the study of the bulbar nerves in order to determine the sensory and motor elements which form the functionally active cranial pairs. It is possible that this character may have some importance, but it is not absolute. Recurrence may be met with not only from sensory nerve to motor nerve, but from sensory nerve to sensory nerve (Arloing and Tripier).

3. **Generalization of the fact.**—Through the labours of Arloing and Tripier, the question of recurrent sensibility has been at the same time extended and renewed. Recurrence of sensory fibres is not a fact peculiar to the motor roots, but is much more general. It is not merely a device to render sensitive the medullary or deep membranes, but it occurs in the distribution of sensory nerves in the skin itself and plays an important part therein. *The more nearly the cutaneous investment is approached, the greater is the importance and the extension of this recurrence.* It here presents also a new character: instead of being confined to the area of a nerve trunk, it mixes the extremities of the sensory fibres over a more or less extended surface.

Experiment.—One of the most striking experiments of these authors is the following: in a dog the four collateral nerves (the two palmar and the two dorsal) of one of the digits of an extremity are uncovered. These nerves are successively cut, and after each section the sensation of the digit is investigated. After section of the first, of the second and of the third, sensation is found to be dulled, but the digit does not present any area which is completely anæsthetic. But if the fourth nerve be cut, the whole digit becomes completely insensible. The conclusion to be drawn from this experiment is that the four collateral nerves have not individually an area of distribution, but that they interchange their fibres by means of the terminal anastomoses which anatomy proves to exist between them. These anastomoses are the result of recurrence; for, after section of one of the nerves, the method of degenerations invariably shows the presence of a small number of degenerated fibres surrounded by healthy fibres of the central end, and conversely.

Applications.—These facts, well established both anatomically and physiologically, supply a plausible explanation of persistence, or of rapid return of sensation, after section of more or less important nerve trunks (median nerve), consecutive to nervous suture, as well as in the absence of the latter. The

re-establishment of sensation is probably due to the fact that the apparent area of distribution of the cut nerve is invaded by fibres of neighbouring nerve trunks, thanks to the recurrent anastomoses which are so numerous at the periphery.

4. **Recurrent motricity.**—The same reasons which cause certain fibres of the posterior roots to re-ascend in the anterior roots, in order to supply sensation to the corresponding medullary area, should also cause certain fibres of the anterior roots to re-ascend in the posterior roots, in order to supply motor power to the organs of movement which are present in the interior and at the surface of the spinal cord. Just as sensation, so is movement everywhere, under a visible or invisible, mechanical or molecular form. Visible movement occurs in the spinal cord (as in the brain), since it contains (as does the latter) contractile vessels to which vaso-motor fibres are supplied. Independently of the invisible movements, there are intrinsic activities in the fixed cells of its membranes, exchanges with the surrounding blood which imply stimulation and a direction imposed by the motor portion of the nervous system.

Remark.—Sensory and motor elements thus arise from the spinal cord, and, after a more or less lengthy course outside the latter, they return to it, having their point of termination (or being able to have it) quite close to their point of departure. The centre and the periphery are thus united in the same organ, and this organ is the spinal cord. Nothing more clearly renders evident the fact that these expressions, *centre* and *periphery*, have merely a relative and conventional value. It is important to remember, indeed, that the two words are used sometimes in an anatomical and concrete sense, sometimes, on the other hand, in a metaphorical and abstract sense. In a differentiated system, such as is the animal organism, every organ, every constituent part is, in virtue of its differentiation into a given order of functions, a centre for other parts, which we then call the periphery, for want of a better word ; and reciprocally.

The prolonged course of these fibres, which leave the spinal cord in order to return to it, seems contrary to the arrangement which governs the living organization ; but this course is rendered necessary by a reason which is of embryological nature. The origin of the sensory fibres is in the spinal ganglia, that of the involuntary motor fibres is in the great sympathetic ganglia : it is necessary that they pass through these ganglionic masses, wherever they come from or whither they go.

Vulpian has investigated this recurrent motricity by exciting the peripheral end of an anterior root while observing the state of the circulation at the surface of the spinal cord in its corresponding segment. He has not noticed any change. But it is possible that the vaso-motors of the spinal cord, like those of the brain, have in the sympathetic chain a more or less considerably prolonged course, the result of which is that, leaving by an anterior root (or even a posterior root) of the dorsal region, for example, they re-enter the spinal cord by a posterior root (or even an anterior root) of another region situated above or below.

Decisive experiment.—When the sympathetic is stimulated in the neck and when, as has been observed by several authors, changes are noticed in the vascular supply of the brain (dura mater or cerebral substance), it is a question,

fundamentally, of a motor recurrent phenomenon. Having started from a nerve centre, which is here the spinal cord (which may receive it from the brain), the motor impulse has returned in the interior of a nerve centre (the brain) to the motor elements which the latter contains; there can be no doubt that it returns in a similar way to the vessels of the spinal cord, by routes which remain to be exactly defined.

3. Conventional Definitions; The Sensory and Motor Field

The posterior root is called sensory, not that it exactly feels, but because it arouses sensation in a system which follows it; the anterior root is called motor, not because it moves, but because it gives rise to a movement in the organs situated at its extremity. What are the exact limits of the sensory system, and where does the motor system commence? Formerly it was maintained that in the spinal cord, and afterwards in the brain, was situated a posterior area, sensory in function, and an anterior area, motor in function; both, in a way, being a continuation of the roots, which were prolonged without any great alteration as far as to the two extremities. But the data furnished both by anatomy and by physiological experiments in no way confirm such a supposition.

1. Comparison of the posterior and anterior portions of the spinal cord and of the brain.—So far as concerns the spinal cord, sensation may be aroused if certain tracts are irritated, and as the result of irritation of certain other tracts movements may ensue; yet these phenomena are far from reproducing quantitatively and qualitatively those which are due to stimulation of the roots. As concerns the cerebral cortex, the sensory and motor areas, instead of being disposed in different departments, seem to be superposed, which would appear to confirm the view of a cyclic process substituted for that of an isolated localization of sensation and motion.

Indefinite limits of sensation and of motion.—It is consequently impossible to point out exactly where sensation ceases and motion commences, the passage from one to the other being gradual. All that can be said is that, *from the organs of the senses to the brain the development of the psychical phenomenon of sensation is progressive; while from the brain to the muscles it follows a retrograde course*, ending by external movement. The former of these roots are *ascending*, and the custom of calling them *sensory* has become widespread: the others are *descending*; they are generally called *motor*. At the present day it would be impossible to change these names for any better adapted for the purpose; but it must be remembered that they have but a conventional value, and that the difference of function which they

indicate progressively diminishes in proportion as we approach more nearly to the cerebral cortex.

With regard to the impulses which it receives, the nervous system first acts as a distributing agent, in its superior regions so singularly called centres, later as a concentrating one upon the organs of movement.

The old criteria.—The cause is easily recognized which at first embarrassed authors in their efforts to define and classify the functions of the spinal cord and brain, and above all of the cerebral cortex. They were convinced that motion excluded sensation, and that, reciprocally, sensation excluded motion. As a matter of fact, these two functions are on the contrary confounded and inextricably mixed. According then as one or other of these two phenomena chiefly attracted their attention in some nervous assemblage, they elected either for sensation or motion. When, for example, with Schiff and François-Franck, the surface of the brain is compared to a sensitive surface, like the skin, the analogy is very true from the purely experimental point of view, but from this point of view only, because it deals with a very special case, that, namely, in which the cerebral cortex being put out of action as an apparatus capable of transforming the impulse, this latter need be only reflected to the spinal cord in order to reach the motor organs properly so called. But if, the cortex being intact, the impulse arising from the skin passes through the latter, new characters are imposed on it by reason of this transit, and these markedly surpass those which are acquired in the spinal cord.

In the double journey which it makes, the one ascending (from the spinal cord to the brain), the other descending (from the brain to the spinal cord), the impulse proceeds from reflection to reflection, or, better, from transformation to transformation; but these transformations have very unequal values in the spinal cord and in the brain. When the impulse proceeds from the first of these organs to the second, the sensory character predominates, as is proved by the absorption of the impulses which ensues in the brain without any motor effect resulting; when the impulse descends from the second to the first, the motor character is that which predominates, yet it cannot be said that it is entirely dissociated from sensation, inasmuch as it recalls the latter in its inferior degrees.

For the *absolute* meaning that these two words "sensation" and "motion" have up to now preserved, it is necessary to substitute a *relative* one, which alone corresponds to the real state of affairs; for the *opposition* which they expressed a *gradation* must be substituted, a *progression* which connects them the one with the other; but as, in the absence of expressions which indicate the different values of this gradation, the old terms are indispensable, we shall describe by the term *sensory field* all that part of the nervous system in which sensory characters predominate over those which are motor, and *motor field* all that region in which motion predominates over sensation. Arbitrary as it is, this definition is founded on fact.

Sensory and voluntary excitation.—Our own powers of observation show us that sensation may exist in us independently of muscular movement, and they further tell us that movement may originate in us in an apparently spontaneous fashion under the influence of certain determining factors which we call *voluntary*. In interpreting these two facts, it seems to have been often thought that sensation is localized at the termination of the ascending conductors, and the will at the origin of the descending conductors, just as if a plane of division existed between these two which could be clearly defined in the nervous system. In reality the arrangement is by no means so simple.

(1) When an actual sensory impulse is only reflected on the muscles, we have no reason to believe that it is stopped at the ideal plane which has just been

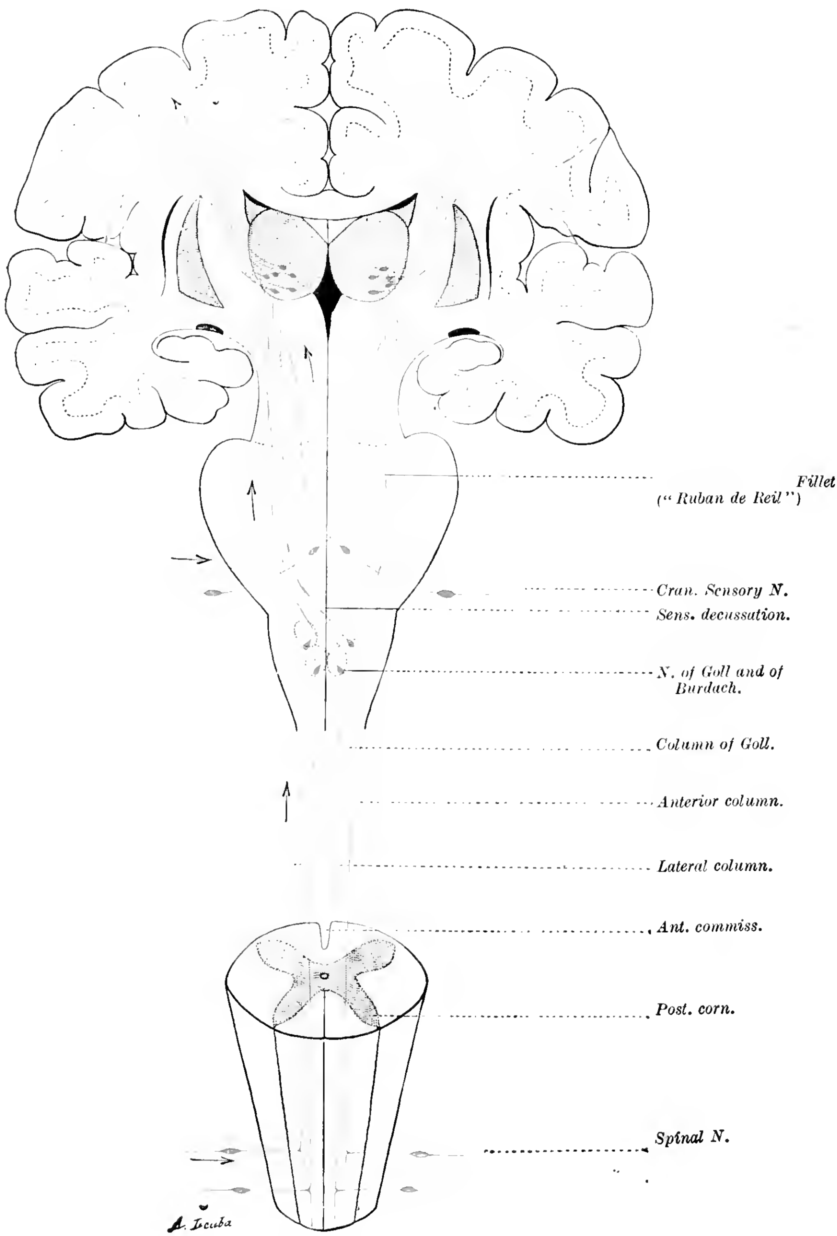


Fig. 52.—Sensory field with its two chief orders of fibres of projection.

referred to; on the contrary, we have cause to think that it often goes beyond this boundary. If, indeed, it does not produce immediate movement, it usually

produces *a tendency to movement* (sometimes slight tension, of the muscles),

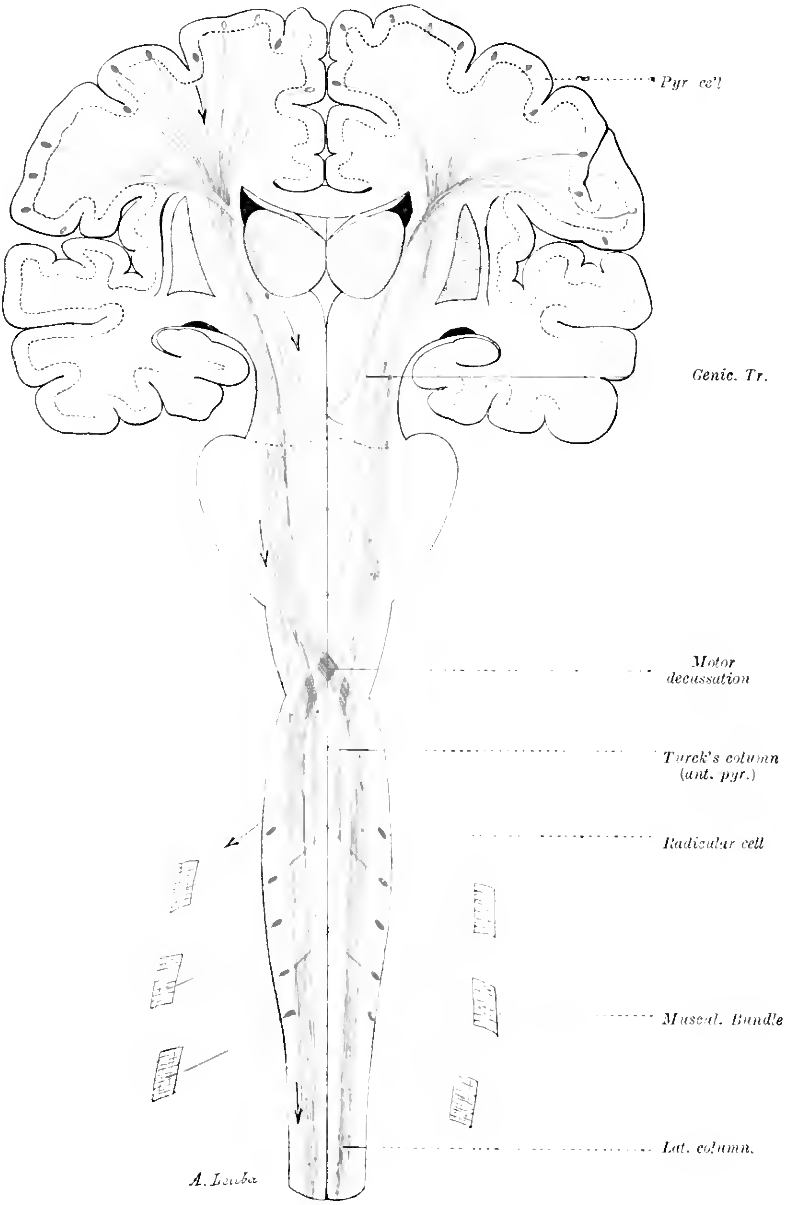


FIG. 53.—Motor field, with its two principal orders of fibres of projection.

arrested in its effects by antagonistic influences situated in the very interior of the nervous system.

(2) When, on the other hand, the muscles are put in action by a voluntary

excitation we have no reason to believe that this latter arises in this plane of separation, and we are justified in maintaining that it proceeds from the nervous conductors which precede it. It arises, in fact, from a memory which is equivalent to *a resuscitation of anterior sensory excitations.*

In the first case, the impulse, after having traversed the ascending paths, is extinguished in the course of the descending paths, without reaching the muscles: its effect is not lost, but it is postponed.

In the second case the impulse, which traverses the descending paths in order to reach the muscles, still proceeds from the ascending roots, but not from their origin in the organs of sense. It pays the arrears of anterior excitations kept in reserve in the nervous system, especially in the brain.

In the two cases the exciting cycle is formed in that part of the nervous arc which is called superior, that which gives to the phenomena of innervation their psychical value, and which is localized in the brain, although no precise limits can be assigned to it.

Is not the process which maintains the impulse in the brain in a condition which may be described as potential itself of a cyclic nature, intended to store it up and causing it to reappear in an automatic and unconscious fashion? We may certainly ask this question, considering the generality of the process and the slight expenditure of energy which nerve actions require. But the verification of such a hypothesis is so far incapable of being effected experimentally.

Double difficulty.—The difficulty which attends the analysis of the functions of the spinal cord and brain is double. The first arises from the fact that the motor and sensory characters, which are so clearly recognizable at the two extremities of the cycle, gradually change in proceeding from its origin to its termination. The second is due to the fact that the nerve elements which represent these functions more or less modified, instead of remaining separate one from the other by forming distinct bundles as in the roots, are often intermixed, fibre by fibre. Further, this intermixture begins in the roots themselves.

2. **Mixture of the sensory and motor elements from the medullary roots.**—The distinction of the peripheral elements of the nervous system into two classes, of which one carry the impulse into the nervous system and the others convey it away, is an absolutely fundamental principle of physiology, and one which has never been contradicted. Nevertheless, experiment does not demonstrate it in that clear and definite manner in which it appeared to the first observers, because these latter were ignorant of certain complications which have since their time been revealed in the nervous organs (roots) which they regarded as simple, and these complications alter, as concerns its anatomical enunciation, the primitive formula of the law of Magendie.

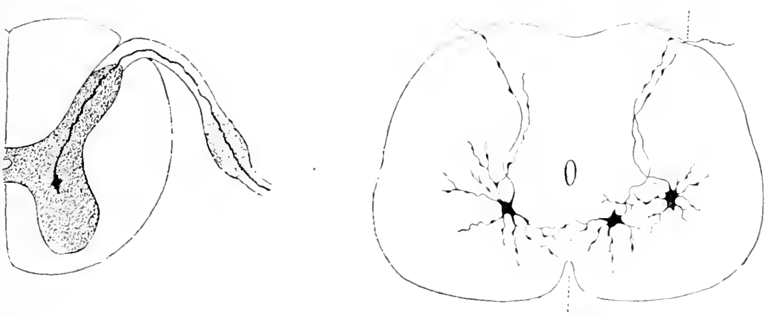
In other words, the distinction of peripheral elements into centripetal and centrifugal is not demonstrated at the present time by a single crude experiment, but is deduced by reasoning which is based on a varied assemblage of experimental facts.

Nevertheless, amidst these secondary facts the experiment of Magendie remains so convincing, that it is customary to place these latter on one side, by giving to the anatomical terms (posterior and

anterior roots) a symbolical value equivalent to that of centripetal and centrifugal nerves.

Structural complications.—Nerve trunks exclusively formed of identical elements do not exist in the organism. The spinal nerve roots represent those of these trunks which the most closely approximate to this simplicity, but without, however, attaining it.

Mixed functions of the posterior roots.—The posterior roots, composed almost entirely of centripetal elements, *contain a very minute proportion of centrifugal elements.* Anatomy proves this by its own special methods. The posterior roots contain neurons, which have the morphological character (polar orientation) of centripetal elements (Lenhosseck, Cajal). The method of degeneration confirms this. After section of the posterior roots some healthy fibres are found amidst those which are degenerated in the medullary end, and in the ganglionic end some degenerated fibres in the midst of the large number of sensory fibres which are still healthy: this proves that the posterior



FIGS. 54 and 54A.—Motor fibres of the posterior roots.

On the right, drawing from nature (Van Gehuchten) from the embryo of a fowl; on the left diagram.

root contains elements whose trophic centre is in the spinal cord (Morat and Bonne).

3. **Physiological proofs.**—If, after having laid bare the lumbo-sacral roots (in the dog), one of them be selected (the sixth lumbar, for example), and be cut in its course, and if the peripheral end be irritated, it will be observed that the temperature of the corresponding hind limb rises considerably (Stricker, Gärtener).

If an animal be chosen whose skin is not pigmented, and the colour of the pulp of the toes be examined after careful washing, it will be seen that this colour progressively darkens while the excitation continues, the former colour reappearing when the excitation ceases

(Morat) ; this is a proof that the nerve trunks contain a certain proportion of *vaso-dilator* elements. Section of the posterior roots is followed, after a certain time, by *trophic disturbances*, such as cutaneous ulceration, falling of the nails and of the hair, thickening of the skin and of the skeleton, chiefly at the extremity of the limb, disturbances which are in reality explicable neither by vaso-motor changes nor by those of sensation (Morat).

These phenomena are motor and as such under the domain of the centrifugal nerves, but their motricity is of a special kind unknown at the time of Magendie, when no other motion was known than that which was voluntary, and at the same time external and evident, of the muscles of the skeleton.

Root elements of one system mixed with the intercentral elements of another.—When applied to the nerve roots, the expressions *posterior* and *sensitive*, *anterior* and *motor*, are precisely equivalent, on one con-

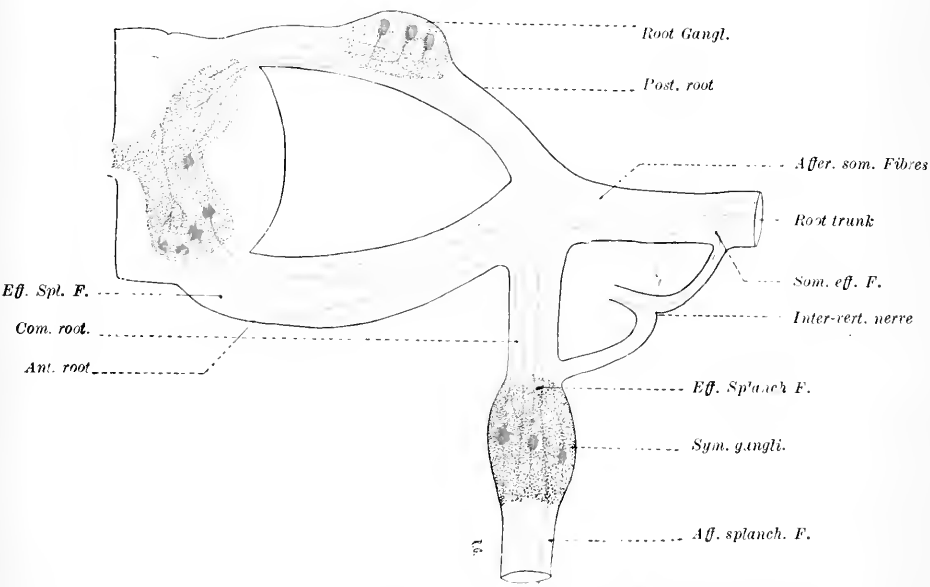


FIG. 55.—Spinal nerve roots, great sympathetic, mixed nerve.

Division between sensitory (blue fibres) and motor (red fibres).

After their intermixture at the meeting point where the mixed nerve arises, there is a fresh division between consciousness (somatic fibres) and unconsciousness (splanchnic or sympathetic fibres).

Structural complications arise from the presence of centrifugal elements in the posterior roots, from the presence of sensory recurrent fibres in the anterior roots, from the presence of recurrent sympathetic fibres involved in the inter-vertebral nerve, and finally from sympathetic fibres joining the somatic nerve (not indicated).

dition : this is that the sensation is conscious and the movement voluntary. When it is a question of movement and sensation of

visceral organs, these expressions are no longer equivalent. As a matter of fact, as will be explained farther on, the medullary roots only merit the name of *roots* as regards a portion of the nervous system, that, namely, which is known as the voluntary conscious side, or that of animal life; as regards another portion, which is the involuntary, unconscious side, and which is represented by the great sympathetic, they are no longer roots, but *intercentral fibres*, extending from the ganglia of this system to the spinal cord, which they bring into reciprocal relation by exchange of impulses; and, being such, they already present those intricacies which render the study of the central masses of the nervous system so extremely difficult.

Spinal roots or those of the conscious voluntary system, and ganglionic roots, or those of the unconscious involuntary system.—The roots of the great sympathetic must not then be sought for in the spinal cord, but outside its ganglia towards the periphery. It is proved (more especially by histological investigations) that neurons arranged inversely place these ganglia in connexion with sensory surfaces and motor organs. Indeed, these two effects may be physiologically dissociated by stimulating comparatively the central and peripheral end of a sympathetic branch after the latter has been cut; but, in the sympathetic, fasciculations which effect an anatomical dissociation of these two species of nerves, comparable to that of the medullary roots of the system of the life of relation, are nowhere to be found.

B. SPINAL NERVES. METAMERISM

The repetition of the roots of the nerves, which are arranged in graduated order throughout the length of the spinal cord, with identical characters and connexions, is a fact which of itself would arouse attention. When connected with the form of the skeleton in the adult, and, above all, with the facts furnished by embryology and by comparative anatomy, it assumes a high degree of significance. Moquin-Tandon (1827) had termed *zoonites* those segments which are so easy to recognize in the external form of many invertebrate animals. Dugès extended this conception to all the ramifications, all animals being, in the early stage of their development, formed of parts ranged in series, which, in spite of their reciprocal penetration, preserve the anatomical, and even functional traces of their primitive separation. The metameres of the vertebrate (Hoekel) are nothing more than the zoonites of the invertebrata.

The segmentation which, in the adult, is rendered evident by the repetition of the medullary roots and of the ganglia of the great

sympathetic, is, in the beginning, much deeper; it divides up the muscles, the nerve axis, the skin itself, into distinct territories (myomeres, neuromeres, dermatomeres) which correspond in each metamere.

The osseous skeleton, whose development is slower, reproduces this arrangement in the spinal column, in which it becomes permanent.

To return to the adult: if, starting from the medullary roots, their tracts be followed either internally in the spinal cord or externally towards the plexuses and nerve trunks which arise from them, the metameric disposition seems to have more or less disappeared, as the result of the intricacy of the peripheral nerve trunks and of the enormous expansion of the roots in the medullary tracts. For its recognition it is necessary to make use of the analytical devices which pathology sometimes furnishes in a very perfect fashion.

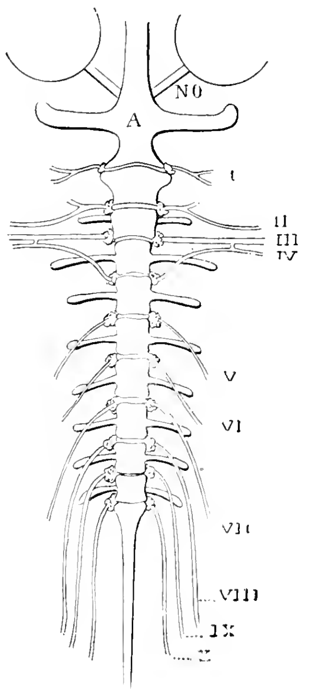


Fig. 56.—Spinal nerves in the frog, and its vertebral column. (front view).

NO, optic nerve, A, atlas; I to X, spinal nerve pairs.

1. **Root and spinal metamerism.**—Brissaud, who has made a special and very exhaustive study of nervous metamerism, distinguishes between a radicular metamerism (that which is rendered evident by the anatomical arrangement of the nerve roots), and a spinal or medullary metamerism (that which is based on the fact that the segments of the spinal cord correspond to the implantation of the roots or myomeres), but he is careful to point out that the one does not in any way imply the other; and the reason of this difference is easy to comprehend. Radicular metamerism is *genuine* metamerism: each nerve pair is a perfect reproduction of the nerve pair situated above and below it. When followed to the periphery, the nerve pair conducts us through territories (cutaneous or muscular) which are, if not entirely independent, at least clearly circumscribed and capable of being defined. On the other hand, spinal metamerism is a metamerism which is *reduced* to a mere trace. The primitively independent medullary segments (as regards phylogenetic as much as ontogenetic evolution) are mutually interpenetrated by their exogenous elements, as well as by those which are endogenous and associating, in such a

manner as to consolidate them for the functions of the whole ; these functions being more extensive, more definite, and more perfect, are substituted for their uniform and rudimentary function ; and the higher we go in the superposed structures of the nervous system, the more obvious will this be. The little independence which is left to the myelomeres is represented by functional connexions which unite, the one with the other, the posterior and the anterior root of the same nerve pair, for the exercise of the most simple reflexes. After isolation of the medullary segment (myelomere), each separate section, furnished with its sensory and motor nerves, can still, in a manner, perform the functions of a partially independent system. Apart from these elementary acts, it is intimately consolidated with the others.

Number of Metameres.—In man there are seven cervical pairs, twelve dorsal, five lumbar, five sacral, one coccygeal.

In the dog, seven cervical, thirteen or fourteen dorsal, seven lumbar, five sacral, several coccygeal.

The spinal cord does not occupy the whole length of the canal, whence arises the existence of a *cauda equina*, as in man.

In the bird there are twelve cervical pairs, seven dorsal, thirteen lumbar, and seven caudal. The spinal cord occupies the whole length of the canal, consequently there is no *cauda equina*, no filum terminale.

In the frog there are ten spinal pairs. The cord is very short with regard to the spinal column, and ends in a long filum.

In man and the majority of animals the dura mater is separated from the spinal cord by a certain space. In the carnivora, especially the dog, the dura mater covers up the cord, with which it is in contact. These two characteristics, the length of the *cauda equina*, and application of the dura mater to the spinal cord, with an extra-dural space filled with fat, greatly facilitate section of the vertebræ, the laying bare of the spinal cord and operations (section, stimulation) performed on the roots in order to determine their functions. In the herbivora, especially in the rabbit, these special facilities either do not exist, or are greatly reduced.

2. **Radicular, cutaneous territories ; areas of anæsthesia.**—If a posterior root is interrupted, an anæsthetic territory (or rather a hypo-æsthetic territory), whose situation and form is determinate, will be found in the skin. This territory is the corresponding dermatomere.

In the case of the roots which run a regular and non-plexiform course, such as the intercostal nerves, it will be easily understood that this territory itself will be regular, assuming the form of zones or of girdles ; but that it should be the same as regards the roots of the lumbar, sacral or brachial nerves, in spite of the plexuses which collect them together, would certainly be more unexpected ; as a matter of fact this is so. If it be conceived that an individual be placed in the position of a quadruped, or rather that the limbs are

separated and perpendicular to the trunk, the skin of this individual may be divided into as many superposed zones as there are nerve

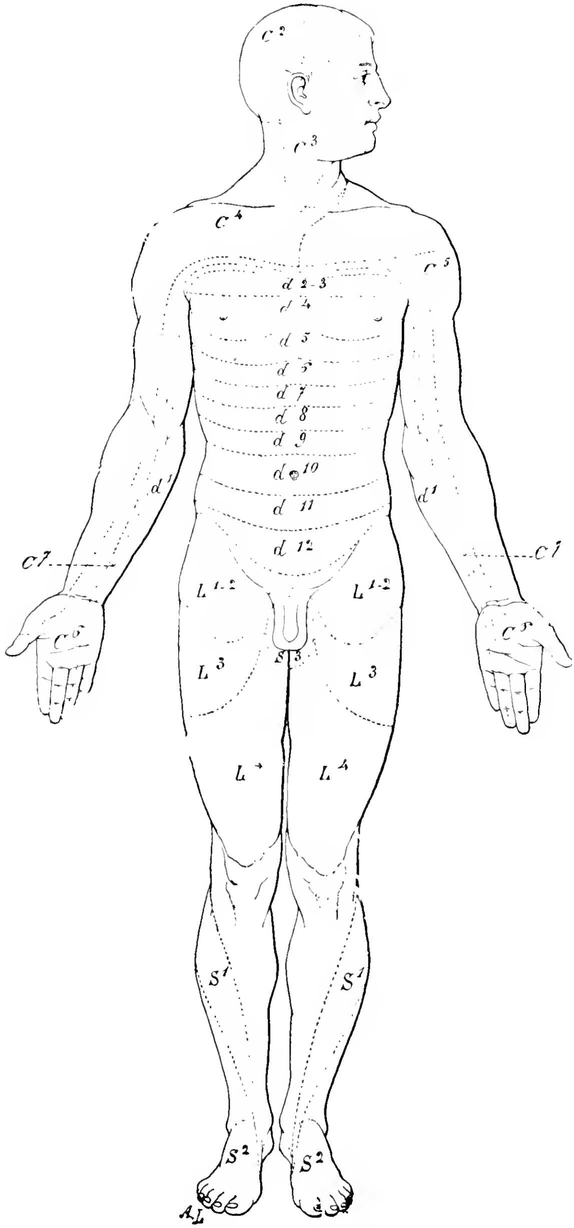


Fig. 57.—Areas of radicular distribution of the spinal nerves (after Kocher). Front view.

pairs (at the least the spinal). The dermatomeres assume the form of circular bands arranged in stages. As regards the upper limb, they

are prolonged along its length in parallel bands, more or less regularly arranged, but continuous. As regards the lower limb, they are always

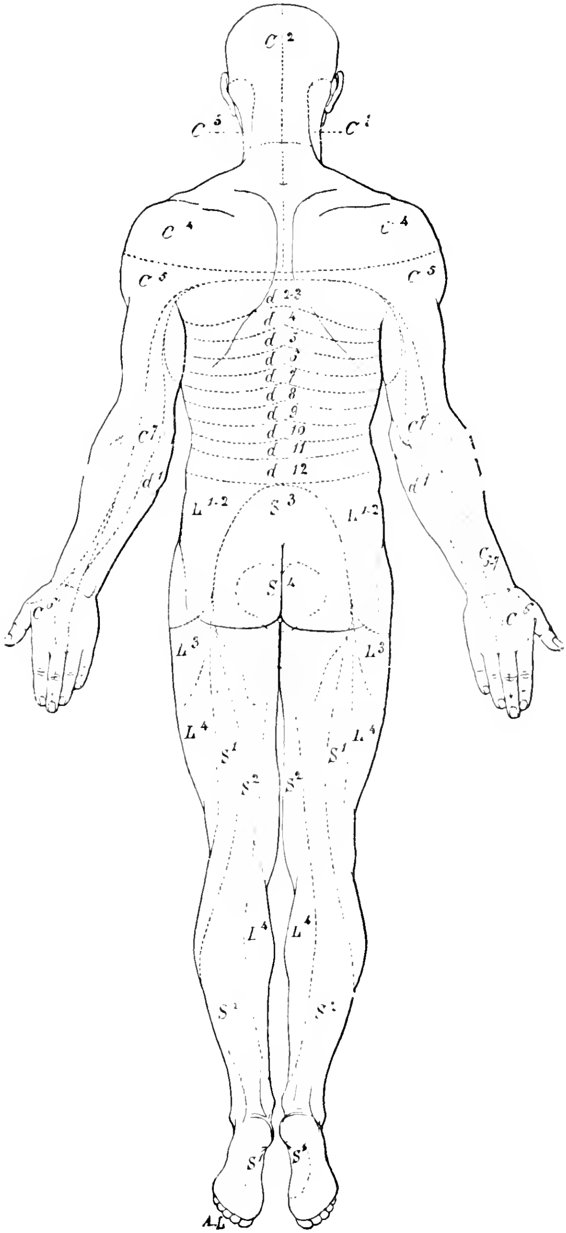


FIG. 58.—Areas of radicular distribution of the spinal nerves (after Kocher). Back view.

placed lengthwise, but are rendered discontinuous by the blurring of

the territories of this region which has been more convulsed during development.

Yet the plexuses are, in a sense, as if they did not exist. The nerve trunks which arise from them (radial, median, ulnar, crural, sciatic, etc.) form an artificial group of root fibres, in which no very definite functional arrangement can be detected. A knowledge of the areas subjected to these groupings is useful when their respective trunks are individually involved by paralysis ; or, again, if it is desired to investigate them experimentally. But the arrangement of these fibres, as regards their course, that is to say, far from their origin and their termination, does not correspond to any real systematization ; on the other hand, the relations of the roots with their dermatomeres is extremely simple, the form of the dermatomere being generally obvious, and their succession in the order of that of the roots themselves.

Mutual interpenetration of the territories.—Such is the very simple scheme of the cutaneous territories as regards their correspondence with the spinal roots. Yet these territories must not be regarded as having determinate boundaries. Every one of them is invaded, at its confines, by the sensory nerves of neighbouring territories (superior and inferior), which are superposed on its own territory, some in one half, others in the other half of its surface. It is obvious that these areas of overlapping increase the size of the area of distribution of each root, but they do not alter the general form of this area, as it is easy to understand. It merely follows that isolated section of a posterior root will in no case lead to the precise and definite anæsthesia of a dermatomeric cutaneous band ; to express the matter more clearly, experiment having shown that it is as described, it has hence been concluded that overlapping zones must exist. Thus the isolated section of a single posterior root will not point out to us its area of cutaneous distribution.

Warned by this experimental fact, Sherrington has overcome the difficulty by allowing a single root to remain intact, amongst several others which have been cut, either in front or behind it (in animals). In this way a sensitive zone is defined (that of the root which has been spared) between two anæsthetic surfaces.

In man, who is able to give an account of his sensations, as the result of multiple or isolated lesions of the roots (confirmed by autopsy), there may be observed, not merely total paralysis, but diminution of sensibility, which is the consequence of it, and in this way it may be possible to deduce the topography of individual radicular innervations (Thornburn, Allen Star, Head).

The results thus supplied clinically agree fairly well with those furnished by physiological experiment.

3. **Radicular muscular territories.**—Isolated stimulation of a motor root causes the contraction of several muscles, sometimes of a fairly large number, according to its size and the number of its component elements. Hence it has its own special territory of motor action, just as the corresponding posterior root has its sensory territory on the surface of the skin. The first is far from having the regularity of the

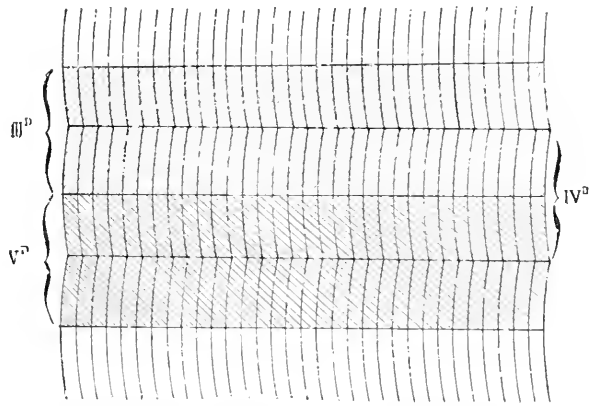


Fig. 59.—Distribution of the sensory fibres of the thoracic nerves (diagram) (after Sherrington).

The areas of the III^e and the V^e dorsal join each other by each overlapping half of the intermediary territory of the IV^e.

second. On the other hand, *each muscle individually generally receives motor elements from several neighbouring anterior roots;* thus it follows that the territories of motor muscular innervation interpenetrate (like the sensory zones of the skin), and this interpenetration has no longer in the myomeres, the regularity which distinguishes it in the dermatomeres.

From the practical point of view (diagnosis of motor paralysis, surgical intervention in nerves), a series of tables may be constructed, displaying, by a given number, the muscular area to which each anterior root is distributed, and the cutaneous territory presided over by each posterior root. So far, treatises on anatomy have preferably prepared tables which point out the field of muscular and cutaneous distribution of the nerve trunks (radial, ulnar, median, crural, sciatic, etc.), arising from the plexuses, that is to say, after the intermixture of the roots in these plexuses, and which are of use in the case of lesion of the trunks, or of surgical intervention in connexion with

them. A knowledge of the second in no sense dispenses with that of the first; because, as is thus seen, they are not superposed in any way.

A radicular trunk is not a functional unity.—Have the roots which numerically follow one another at the origin of a nervous whole, such as the brachial plexus, individual special functions, such as extension, flexion, adduction, abduction, for the motor roots of the superior extremity? Ferrier and Yeo, P. Bert and Marcacci, who were the first to study this question experimentally, have answered in the affirmative. But their results have been contradicted by Lannegrace and Forgue, who have not been able to find between each motor root and its muscular territory anything beyond a purely anatomical or topographical correspondence, without any suggestion of function. The component elements of the same root resemble one another, in that they all possess a motor function; but these elements enter into the complexus, which makes use of their function in a variety of ways. The natural movements, even the simplest, imply, indeed, an action which is at the same time gradated and successive of the muscles which execute them; in other words, in order to effect the movements, a co-ordination both as regards time and space of the contraction of these muscles is necessary; this is the result of associations, carried out in the grey matter, between neurons which are more or less approximated or separated, and hence which do not necessarily belong to the same group of original cells giving origin to a root.

Dissociation of the root in its bundles.—In fact, the total artificial excitation of an isolated anterior root may certainly produce a defined movement in the corresponding limb (flexion, extension, adduction, etc.), but this is simply due to the fact that, the excitation acting upon a collection of fibres whose functions are different or antagonistic, the resulting effect arises as regards the strongest muscle, or that which receives the strongest stimulation.

If, as Russell has done, an anterior root be dissociated into its component bundles, and each one of these be separately stimulated, different and sometimes antagonistic movements will be aroused by these localized excitations. This proves *that the same root is distributed to several muscles whose function, further, is not univocal.* Conversely, *the same muscle receives the fibres of several roots.* Practically, these results explain how it is that isolated paralysis of an anterior root only causes transitory disturbances of movement.

These facts are in agreement with those of the same order observed clinically (Allen Star, Mills, Kaiser).

4. **Mixed nerves.**—The anterior and the posterior roots intermingle

their fibres just beyond the spinal ganglion, and thus form a *mixed nerve.*

At the spot where the mixed trunk of the nerve pair emerges from the inter-vertebral foramen it receives from the ganglia of the great sympathetic sensori-motor elements of a new order, which still further complicate its composition. Thus it is mixed, not only by the addition of sensory and motor elements, but also by that of elements possessing different varieties of sensation and of motion.

Thus constituted and completed, the mixed trunks to which the nerve pairs give origin extend to the periphery, where they are distributed to definite territories which are arranged in gradated order corresponding to that (or nearly so) of the roots from which they arise.

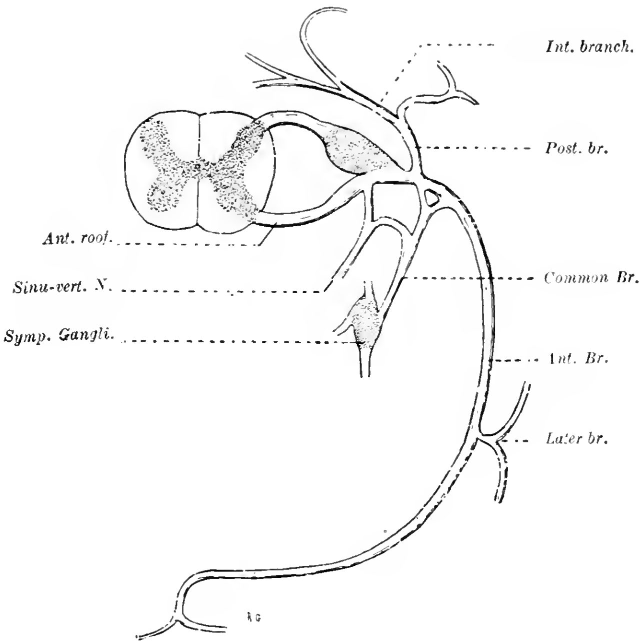


FIG. 60.—General arrangement of a spinal nerve (diagram).
An intercostal nerve is taken as a type.

These territories are, some, cutaneous (*dermatomeres*); others muscular (*myomeres*), and yet others visceral (these may be called (*splanchnomeres*).

Definitions and Distinctions.—These divisions are not so absolute as would at first sight appear. The skin does not wholly represent the tactile sense, of which, it is true, it is the accredited organ; the viscera penetrate it to a marked degree under the form of vessels, glands or other organs, whose function is unconscious

and involuntary. The muscles do not represent solely animal movement ; the vessels equally penetrate them ; and, further, a kind of sensation is acquired by them which is intermediate between that of the skin and that of the viscera. As regards the viscera, properly so-called, if they send prolongations to the skin and the muscles, they do not in return receive anything from these organs, to which they serve as a fundamental and indispensable base. The words *dermatomere, myomere, splanchnomere,* will thus possess different senses, according as to whether the essential function, or the totality of the functions, which are represented in them are considered ; according also as to whether the essential part of an organ, or the prolongations which it furnishes to others, is taken into account.

The constitution of the metamere, above all, that of its nervous system, explains these distinctions. The really fundamental portion of this latter consists of the ganglia of the great sympathetic. From the vertebral ganglion branches arise which proceed to the viscera, and which, following the vessels wherever they penetrate, finally attain the whole field of the metamere ; this is the origin of the vegetative system. As regards the intestine (and the large viscera), these branches continue isolated. As regards the skin and the muscles, they are indeed duplicated by others, which skirt them, and which represent conscious sensibility and voluntary movement : this is the origin of the animal system. Their origins are distinct from those of the preceding, and are in the spinal ganglia and the grey matter of the spinal cord. They accompany the sympathetic branches (as they become preponderant, it is generally said that they are accompanied by them) in the myomere and the dermatomere. They form with regard to the others a supplemental and perfected, differentiated system. They assume the function of external life, and from this fact have nothing in common with the viscera, which are organs of nutrition, while the converse is not so.

When, in order to define the portions of the nervous system which (development being finished) have retained the metameric arrangement, we call the roots, *medullary*, we omit an important portion of the nervous system which has preserved this disposition ; these are the branches (direct or intermingled with the mixed trunk) which arise from the ganglia of the sympathetic chain, and which have the same distribution as the corresponding roots. On the other hand, when, in order to furnish an example of true metamerism, we bring forward these same roots, the designation is only correct so far as we restrict it to the conscious voluntary elements of these roots ; these alone obey the usual laws of metamerism, while the unconscious or vegtative elements elude them. These latter indeed have not, like the first, a direct course from the segment of the cord to the peripheral nerve for which they are destined by the corresponding roots ; but, arising either above or below the ganglion which collects them, they pass for a certain distance vertically into the chain of the great sympathetic. *The chain of the sympathetic destroys the metamerism of the vegetative system, just as the organization of the spinal cord destroys that of the animal system.*

Trophic disturbances.—Among the facts which indicate metamerism of the nervous system, trophic disturbances of the skin have often been emphasized. Trophic troubles are motor phenomena of a special order. It is proved, both experimentally and clinically, that, in many cases, their appearance depends on the nervous system. The existence of nerves whose function is solely and specifically trophic is no longer admitted, but trophicity is regarded as a function of the nervous system. The disorders of nutrition may sometimes affect the same distribution as the areas of anæsthesia ; some are accompanied with pain, as for instance, *herpes zoster.* These peculiarities have led to them being regarded as arising from an alteration of the sensory trunks, especially the ganglia of the posterior roots (Baerensprung). It has been thought that from this alteration

of the sensory nerves it would be justifiable to infer the origin of the nervous action; in this case the action would be strongly *reflex;* and would be reflected on the skin (Brissaud).

Centrifugal cutaneous nerves.—But the posterior roots contain centrifugal fibres; and it is possible that certain of these fibres proceed to the fixed elements of the skin, just as there are those which go to the glandular cells of this structure. The alteration of these fibres and the perversion of function in the cutaneous covering, which is the result thereof, leads, in the end, to a modification of its structure (trophic disturbance). The areas of these neuro-trophic dermatoses may then be superposed on those of the anæsthetic zones, if, as is probable, the centrifugal fibres of the posterior root have, more or less accurately, the distribution of the centripetal fibres of the same root.

Segmentary alterations of sensation and of nutrition.—Trophic disturbances and partial anæsthesia affect an equally regular form in certain cases, but have an orientation altogether different to that of the preceding. Instead of being *zonal,* the cutaneous lesions are *segmentary.* This arrangement is particularly striking in the limbs (dermatoses assuming the form of a glove, that of a sleeve,

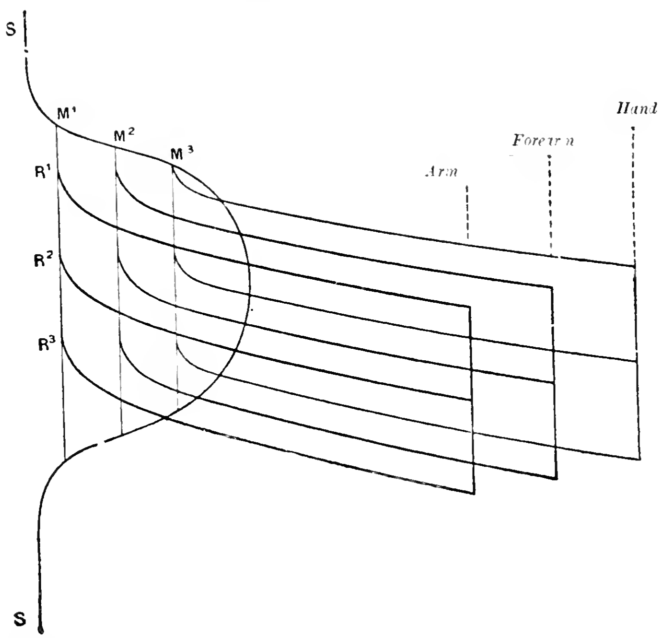


FIG. 61.—Diagram of the metameric and segmentary distribution of the nerves of the upper limb (after Brissaud).

The cervical enlargement of the spinal cord is divided by horizontal lines into three metameres to which the roots R^1, R^2, R^3, going to the thoracic limb, correspond; by vertical lines into three segments M^1, M^2, M^3, of which the deepest gives off nerves of the arm, the middle one nerves of the forearm, and the most superficial nerves of the hand.

etc.). In order that such forms may be the result of limited lesions of the grey substance of the spinal cord, they must be inscribed there in the arrangement of the origins of the nerves. According to Brissaud, the spinal cord is not only formed of superposed neurotomes (corresponding primitively to the roots superposed in the same order), but its grey matter presents, in its lateral thickness, superadded layers, which reinforce it at the site of equally superadded portions

(which are the superior and inferior extremities) by giving origin to its enlargements (cervical and lumbar). In these enlargements the most superficial layers are those which supply the nerves of the hand or foot ; the deepest, those which furnish the nerves of the shoulder and of the hip. Hence it is easy to understand how isolated alterations of these nerves may give rise to lesions of a form also singular in its regularity. Anæsthesia also is subservient to the same disposition.

Sensory visceral areas.—When the large viscera are the seat of a lesion (especially inflammatory), their ordinarily unconscious sensibility becomes conscious, and we perceive the pathological excitation of their sensory nerves under the form of pain. But this excitation, on arriving at a medullary segment, is (in consequence of its abnormality and of the error to which it gives rise) often *exteriorized in the cutaneous nerves* which terminate in this segment. Head has made use of this circumstance in order to ascertain the medullary segments which correspond to each of the large viscera and to each of their principal portions.

Clinical phenomena of this kind have been long known, for example, pain in the left arm and the left little finger in angina pectoris ; pain in the right shoulder in hepatic colic, that in the testicle in renal colic. Mackenzie has also observed that, in intestinal obstruction, cutaneous pain is situated above the umbilicus, when the obstacle is situated in the small intestine, and, on the contrary, between this point and the symphysis pubis when the obstruction is in a portion of the large intestine.

In order to determine the visceral sensory areas, Head takes into account not merely these painful radiations, but also the *hyperæsthesia* which is obvious in certain cutaneous zones under the influence of slight stimulation (pressure). He has proved the existence of a large number of hyperæsthetic zones, which are very diversely situated, and whose relation to the roots of nerves, and hence, to the corresponding medullary segments, he has endeavoured to ascertain.

The reasoning on which these researches are based is the following : these hyperæsthetic zones (according to Head) can be superposed on the anæsthetic zones which are observed in the lesion of the roots and of the corresponding medullary segments, and whose areas have been determined by physiological and anatomical clinical methods. The hyperæsthetic zone indicates the affected root. Clinical experience, on the other hand, showing that such and such a zone is hyperæsthetic when such and such a viscus is diseased, we are hence justified in concluding that the sensory nerves of this viscus and of the hyperæsthetic zone (although topographically they may be far removed) terminate in the spinal cord in common nuclei. It is these common nuclei which, receiving the pathologically exaggerated irritations of the inflamed viscus, exteriorize them in the skin. This external manifestation may thus become a diagnostic aid as regards the affected viscus.

Such is the principle of this method. Practically it still presents too much uncertainty, and the results have proved too discordant for us to be able to give here a detailed table, this table still requiring very important revision. It may be added that the proofs are too indirect in nature, and lend themselves to too many objections, to be accepted without discussion.

The relations pointed out between the hyperæsthetic zones of Head and visceral lesions may, however, retain their symptomatological value, while still leaving untouched the problem of the systematization of the sensory visceral nerves.

C. CRANIAL NERVES—FUNCTIONAL DETERMINATIONS

1. Morphological regularity of the spinal cord.—In the spinal cord, the origins of the sensory and motor nerves are systematically arranged

in a simple and regular manner, so that they can be recognized at first glance, it being assumed that experiment has determined their functions. *Every nerve pair has its component elements arranged in the same manner, and experiments carried out on one are applicable to all.*

2. **Irregularity of the medulla oblongata.**—In the medulla oblongata this systematic arrangement has disappeared, or has become almost unrecognizable; it is on this account that there is a question concerning the *cranial nerves.* The sensory and motor elements form in it, indeed, irregular groups which destroy the systematic arrangement by which they can be so easily recognized elsewhere, by merely regarding their relative position; hence it is necessary to investigate these elements of diverse function by experimenting directly on each of the nerve trunks which arise from the medulla oblongata.

New superadded formations.—The medulla oblongata is a place of transition; the symmetrical and regular medullary cylinder ends in it; the cerebral expansion commences in it, or is more or less prepared in it by accessory formations. These new masses, of different function and type, at first sight upset the primitive scheme of the medullary edifice. Nevertheless, modified traces of it may be recognized, but for this it is not too much to unite the data furnished by experiment with those of morphology.

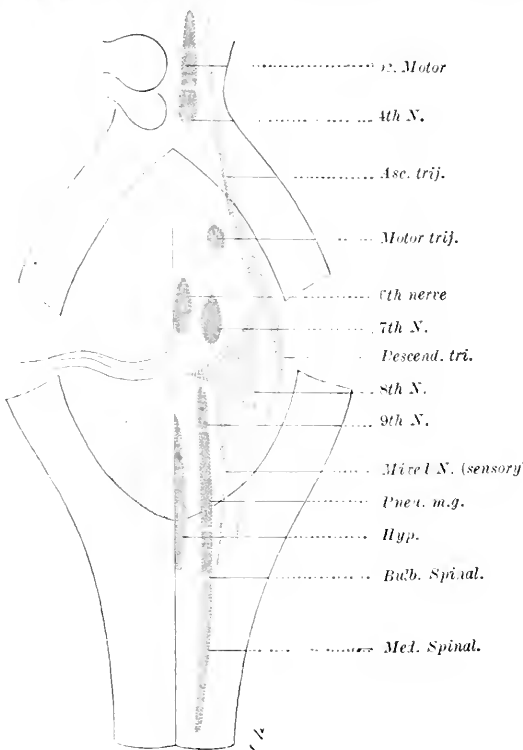


FIG. 62.—Topography of the nuclei of the cranial nerves situated in the floor of the 4th ventricle. The motor nuclei in red the sensory nuclei in blue.

VERTEBRAL THEORY OF THE CRANIUM.—The classification of the cranial nerves is connected with the old theory of Goethe and Oken, a theory often furbished up, and which we will attempt to describe in a few words.

So far as concerns the cranial nerves, there is a double problem: (1) to recognize the equivalents of the anterior and posterior roots; (2) the nerve pairs being constituted, to ascertain their metamerism.

Ventral and dorsal nerves.—In the spinal cord each pair is formed by a *ventral nerve* (the anterior root) and a *dorsal nerve* (the posterior root). The ventral nerve is exclusively connected with the muscles; or, in other words, it is functionally *motor*. The dorsal nerve is connected with the skin; in other words, it is *sensory*. It must be added that in the dorsal nerve some centrifugal elements exist, but in limited number, which thus make it (however small their number and their importance) a mixed nerve.

The ventral nerves (motor nerves) arise from the cells of the anterior cornua, emerge from the ventral path of the nerve axis, and are distributed to the muscles taking origin in the myotomes.

The dorsal nerves (sensory nerves) arise from the cells of the spinal ganglia, penetrate the spinal cord by the dorsal portion of the nerve axis, and are functionally related to the organs of touch situated in the skin. Their motor fibres

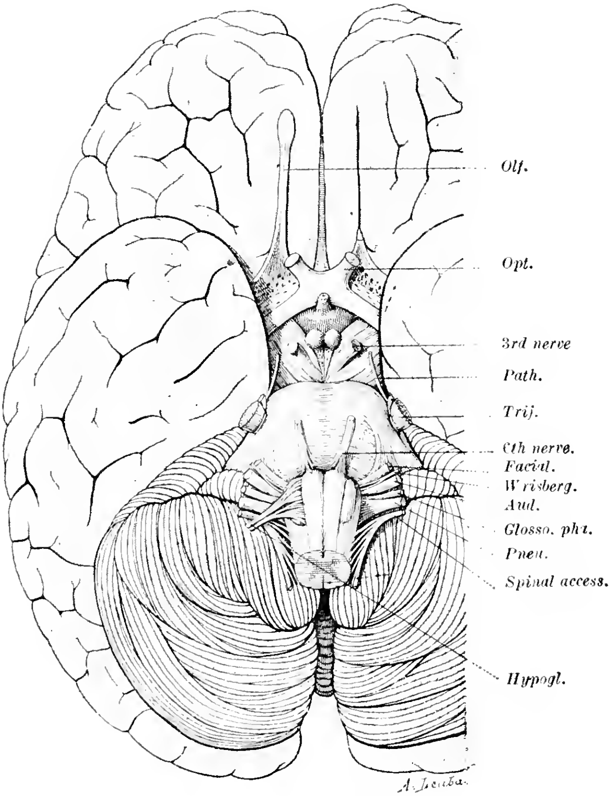


FIG. 63.—Apparent origin of the cranial nerves at the base of the brain (after Hirschfeld).

are very few and have only been studied so far as regards their function in those varieties which make their classification difficult (vaso-motor elements).

In the cranium, the series of ventral nerves would be represented by the motor nerves of the eye (oculo-motor, external oculo-motor or sixth nerve, pathetic or fourth nerve) and the *hypoglossal*. But the fourth nerve is still under discussion on account of its posterior exit; the series of dorsal nerves would be represented by the *trigeminal, the facial, the glosso-pharyngeal, the pneumogastric and the spinal accessory.*

The nerves of special sense are generally left unclassified, on account of their extremely pronounced differentiation.

Comparative morphology.—In the case of man, the arrangement, dorsal and ventral, of these two series is not very obvious, but it is much more so in that of the inferior vertebrata. In any case the ventral series represents those nerves which are, in the cranium, the continuation of those which arise from the antero-external group of the anterior horn of the spinal cord, and which are distributed to the muscles originating in the myotomes. Difficulties and objections arise, on the other hand, when the dorsal cranial nerves are compared with the posterior spinal roots. The motor elements which enter the trigeminal, facial, pneumogastric and spinal accessory, are of such great importance that they can scarcely be compared to the few centrifugal fibres of the posterior roots. Further, while the latter have a connexion only with the skin, the sensory cranial nerves are distributed to the digestive mucous membrane.

Superadded nervous apparatus, branchial nerves.—This difference is explained, according to Kuppfer, by the existence, in the region of the dorsal cranial nerves, of a superadded system, *the system of branchial nerves,* which is wanting in the spinal nerves. This branchial nerve distributes its motor ramifications, not to the muscles derived from the dorsal segmented portion of the mesoderm (somites, myomeres, myotomes), which, in the cranium, as in the head, are innervated by the ventral nerves (eye and tongue muscles ; oculo-motor and hypoglossal nerves), but to other muscles, which are wanting in the trunk and are present in the head, and which originate from the lateral mesodermic nerve, segmented by the branchial clefts.

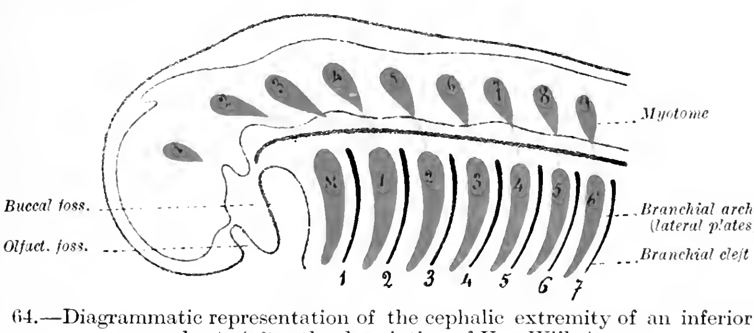


FIG. 64.—Diagrammatic representation of the cephalic extremity of an inferior vertebrate (after the description of Van Wijhe).
The cephalic mesoderm (myotomes and lateral plates) in red.

The dorsal nerves, in the cranial region, are thus the result of the union of a posterior root with a branchial nerve.

Metamerism.—In the trunk, primitive metamerisation of the individual is rendered evident, in the adult, by the vertebral bodies and the corresponding nerve pairs which emerge in the interval between them. In the other organs, including the nerve axis and the whole of the muscles, there is no trace of this arrangement. In the cranium, the skeleton, as also the muscles, are a very untrustworthy and arbitrary evidence if examined in the adult. It is necessary to have recourse to the antecedent arrangements in order to recognize metamerisation in this region, and Huxley, and after him Gegenbaur, find the evidence of this in the disposition of the branchial apparatus, each of the visceral arches of which would correspond to a metamere provided with its nerve pair.

Myomeres and branchiomeres.—But, with Van Wijhe, it is necessary to take into account the segmentation of the cephalic mesoderm, which gives rise, in the skull as in the trunk, to a certain number of somites or myomeres ; and this so much the more as, the strict and exclusive relationship of the somites with the

ventral roots being allowed, we shall thus be supplied with a fixed base for the numeration of the metameres. The solution of the question would be clear and definite were it possible to be certain as to the exact number of the segments. But the rapid changes which ensue in the course of evolution upset at every moment the actual condition, certain of the myomeres falling into a state of atrophy very soon after their appearance. Yet further, the parallelism between the somites and the visceral arches is itself of short duration and gives rise to uncertainty, the myomerism and the branchiomerism not proceeding equally. It thus results that the dorsal and ventral nerves can only be classed separately, without endeavouring to collect them together into exactly corresponding pairs; and hence the determination of the ventral nerves is difficult from the metameric point of view.

(*a*) Physiological characters of the nerve pair.—Physiology, which is based, above all, on the study of function, allots to the constitution of the nerve pair other characters chiefly drawn from experiment. *The nerve pair* is in this respect *essentially made up of elements which are functionally associated in the constitution of a simple reflex axis,* as they are in the metamere. Cl. Bernard emphasized another character, which expresses the signification of the preceding one: *Two nerves, one sensory and the other motor, form a physiological pair, when the first gives to the second its recurrent sensibility.* When it is remembered that, as Cl. Bernard holds, the terminal apparatus of this recurrent sensibility is situated at the surface of the spinal cord and of its membranes regarded as receptive of excitation, in the very region of the roots under consideration, the functional association of the two nerves will be seen to be strengthened.

Contingence of the associations in the course of functional activity.—But the physiologist also knows that these connexions are changeable, according to the progress and the necessities of the functions, and he is therefore the less surprised on learning of the difficulties which prevent a rigid classification of these associations. For him the conception of the nerve pair has a symbolical value, or one for convenience of description. Having made these reserves, it may be useful to point out those amongst the cranial nerves which approach the most closely to the primitive and ideal scheme which has been studied with regard to the spinal roots.

Thus we find, in the *trifacial or trigeminal* those characters which are most clearly characteristic of a sensori-motor nerve pair, but of a nerve pair which has already lost its regularity and its symmetry, and which must be completed or dissociated if it is desired to re-establish in it equilibrium between the sensory and motor elements.

Nerve pair approximating the spinal type.—The trigeminal nerve takes origin in the medulla oblongata through the pons by two roots, the one *sensory,* bearing a *ganglion* (*Gasserian ganglion*), which is

obviously the equivalent of the ganglion of a posterior spinal root; the other *motor*, which proceeds to form with the preceding a mixed nerve by intermingling of its fibres. This is not merely an induction from the resemblance of form; if an experiment is made (with more difficulty, it is true) on the roots of the trigeminal similar to that on those of the spinal nerves, sensory and motor paralysis may be induced by the section of the nerve; by the stimulation of each of the two roots sensation and motion may be elicited.

But this nerve (as its name points out) has three branches, corresponding to the three large subdivisions of the face, and of these three branches the third only (inferior *maxillary nerve*) receives the elements of the motor root. Hence the trifacial pair must be com-

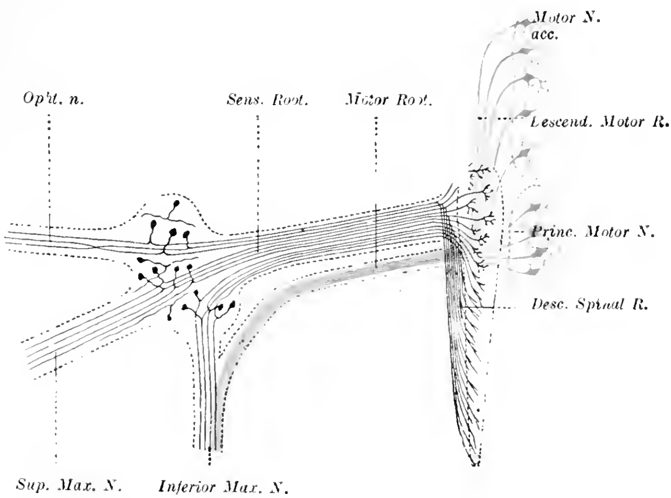


FIG. 65.—Diagram of the real origins and the constitution of the trigeminal (after Van Gehuchten).

pleted by the addition of motor elements. These elements are found in the purely motor trunks, which are distributed to the muscles of the orbit and which supplement the first branch of the trigeminal (ophthalmic branches), which confer sensation on the ocular region; these are the *oculo-motor nerve, the external oculo-motor nerve, and the pathetic.*

Functional association of the radicular elements.—The trifacial pair is obviously sensori-motor. It corresponds to the same sense as the posterior roots, namely, to the *tactile sense or that of general sensation.* The other cranial pairs, more or less strictly so-called, which take origin from the medulla oblongata, have as a basis either purely sensory nerves, as the olfactory, the acoustic, or the optic; or nerves

in which sensorial elements are mixed with sensory elements, as the glosso-pharyngeal; or, finally, trunks in which general sensation is mixed up with obtuse and subconscious sensation, as the pneumogastric and spinal accessory.

Their complexity.—These associations between sensory nerves or those of special sense, and motor nerves, are from the point of view of function, both multiple and variable. Hence they are in no sense exclusive the one of the other. The motor nerves of the eye, which

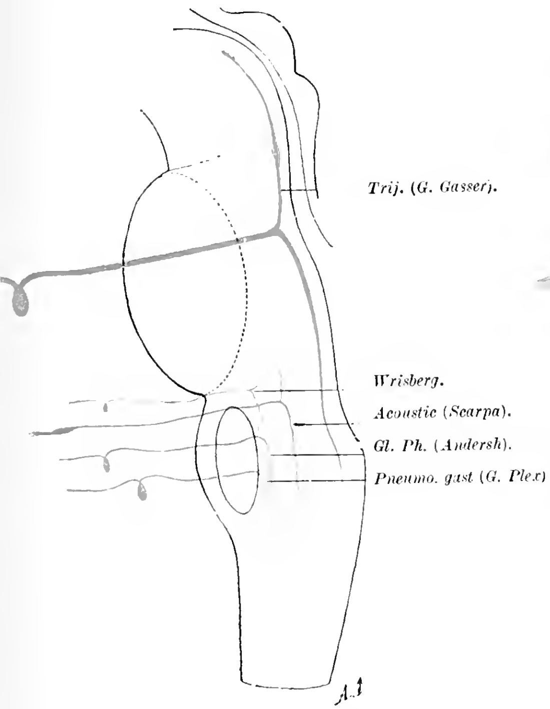


FIG. 66.—Ganglia of origin of the sensory cranial nerves.

Their roots, and the ascending and descending branches of these roots.

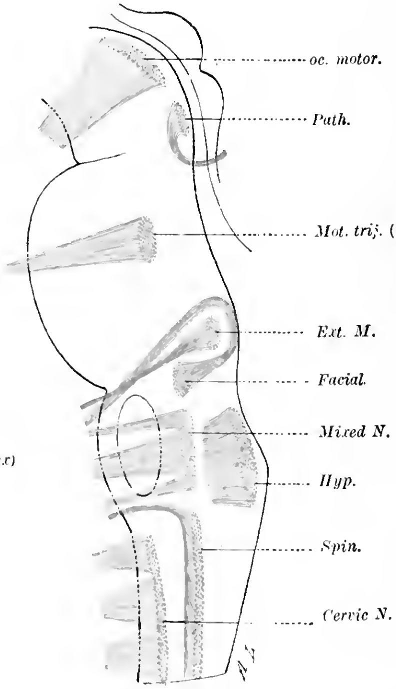


FIG. 66A.—Nuclei of origin of the cranial motor nerves (diagram).

The nuclei are seen laterally through the cerebral trunk supposed to be transparent.

are connected, by the ophthalmic branch of the trigeminal, with general sensation, are equally so, by the optic nerve, with the sense of vision, and may be connected with that of hearing, or of any other by the special conducting tracts of these senses. And it must not be forgotten that it is the same in the spinal cord; the functional bond of union which subsists between the posterior and the anterior root, and which is manifested by a reflex act, is interesting, because it illustrates the rough sketch of the nervous system; but it is not strictly necessary, and the muscles of the limbs or of the trunk, as

well as those of the face, are functionally associated at every moment with the superior senses.

Another example.—The *facial*, with its two roots, of which one (small root) bears a small ganglion (*geniculate ganglion*), is also often compared to a spinal nerve pair.

The large root is obviously motor ; the small, known as the nerve of Wrisberg, is regarded as a nerve of special sense ; it shares with the glosso-pharyngeal the faculty of conferring the sense of taste ; by the chorda-tympani it proceeds to the tip of the tongue, while the glosso-pharyngeal is distributed to the root of the tongue ; the tip and the root of the tongue comprise the area of the sense of taste.

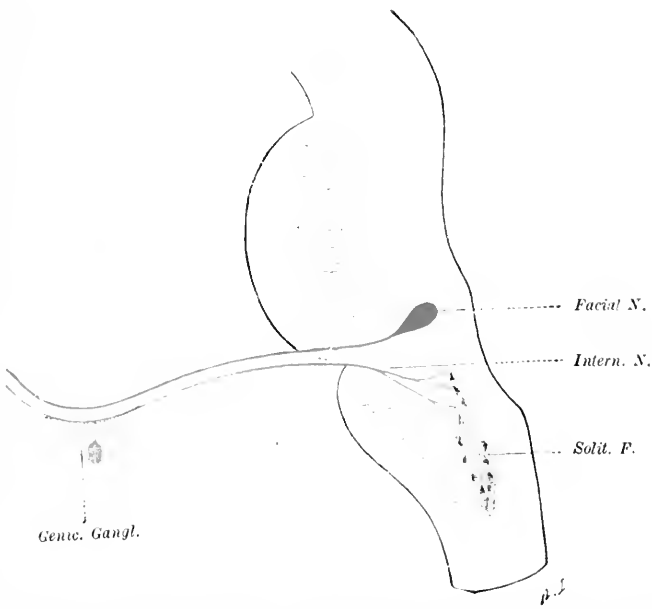


Fig. 67.—Facial nerve and intermediary nerve of Wrisberg. Facial pair.

Multiple associations of the original elements.—The motor portion of the facial nerve does not go to the muscles of the tongue, but to the cutaneous muscles of the face, and it is consequently not connected with the sense of taste except in a wholly contingent manner. The motor portion of the facial is, on the contrary, connected in a more direct manner, although a still very partial one, with the sense of hearing by the branches which it supplies to certain muscles of the ear (muscles of the external ear, muscle of the stapes). The acoustic nerve is closely attached, at its origins, to the two roots of the facial, and passes through the same orifice as the latter (internal auditory meatus) before separating from it in order to proceed to the internal ear. From the functional point of view, the facial is also associated with the sense of smell, in order to ensure the movements of the nostrils connected with the exercise of this sense ; with the sense of sight, in order to perform the movement of the upper lid ; and very generally with the tactile, or general sensibility, of the trigeminal.

The hypoglossal nerve, its small inconstant root.—The motor nerve of the tongue, whose mucous membrane is supplied with the organs of taste, is the hypoglossal. Usually it is formed of a single order of roots (motor roots) ; but

sometimes it is supplied with a small root bearing a ganglion, and thus reproduces the type of the spinal nerve pairs.

Glosso-pharyngeal ; pneumo-spinal.—The glosso-pharyngeal, the pneumo-spinal (formed by the union of the origins of the pneumogastric and of the spinal accessory) originally contained motor and sensory elements of different nature, which have caused them to be assimilated to the functional pairs. Their centrifugal and centripetal elements are mixed from their exit from the medulla oblongata ; the ganglia which they pass through (ganglion of Ehrenritter and ganglion of Andersch in the first ; jugular ganglion and plexiform ganglion in the second) are partially comparable to the spinal ganglia of the posterior roots.

Overlapping and reciprocal penetration of areas.—In short, all the motor, sensory, nerve trunks and those of special sense to which we have just referred are distributed to areas which overlap each other, fit together, penetrate each other, and are more or less superposed ; to such a degree, indeed, that only by experiment is it possible to determine their limits and to unravel the complicated skein formed by every kind of fibre which is woven in the tissues of the face and of the neck through their multiple anastomoses.

As they present themselves to our observation and to experiment in the adult animal, the cranial nerves are, some of them, isolated, such as the olfactory and the acoustic ; while others reproduce, more or less definitely, the arrangement of the spinal nerves (trigeminal, facial) ; others, again, have their sensori-motor elements mixed from their emergence.

Method of study and description.—The method of study of these anatomical groupings is based on a double analysis : (1) it is necessary to separate in them the *sensory* from the *motor* elements : (2) further, to separate in these groups, the different sensory and motor elements. From this second point of view the elements are divided into two new general categories, that of the *conscious* and that of the *unconscious*, as will be explained further on. Anatomically, the unconscious is represented by the *great sympathetic* and its bulbar equivalents. On account of the intimate intermixture of these elements with the majority of these nerves whose anatomical arrangement is morphologically irregular, it is necessary, in order to obtain perspicacity, to now describe the cranial sympathetic at the risk of repeating this description when we commence the study of the unconscious system as a whole.

(*b*) Relations with the Great Sympathetic.—In the spinal cord each nerve pair is attached to a ganglion of the great sympathetic and is, in a way, completed by its connexions with this special system. It is precisely the same in the medulla oblongata ; only the determination of the elements which belong to it presents, in this region, greater difficulties. In fact, the great sympathetic, in its strictly vertebral portion, follows the same typical and regular arrangement as the nerve pairs with which it exchanges communicating branches. In the cranial portion, the shocks which have dissociated the primitive nerve pairs have, at the same time, changed the morphological characters by which they are recognizable, and compel us to identify them by the direct authentication of their functions.

Normal Type of these Relations.—Yet, the normal type of the relations of the great sympathetic with the other nerves has not entirely

disappeared, and it is again in the subordinate divisions of the trigeminal that we recognize it. To the three branches of distribution of this nerve (ophthalmic branch, superior maxillary nerve, interior maxillary nerve) are attached three ganglia (*ophthalmic ganglion, spheno-palatine ganglion, otic ganglion*); further, a fourth ganglion (*submaxillary ganglion*) is attached to a large branch of the submaxillary nerve, the lingual nerve, all of these ganglia being clearly those of the great sympathetic.

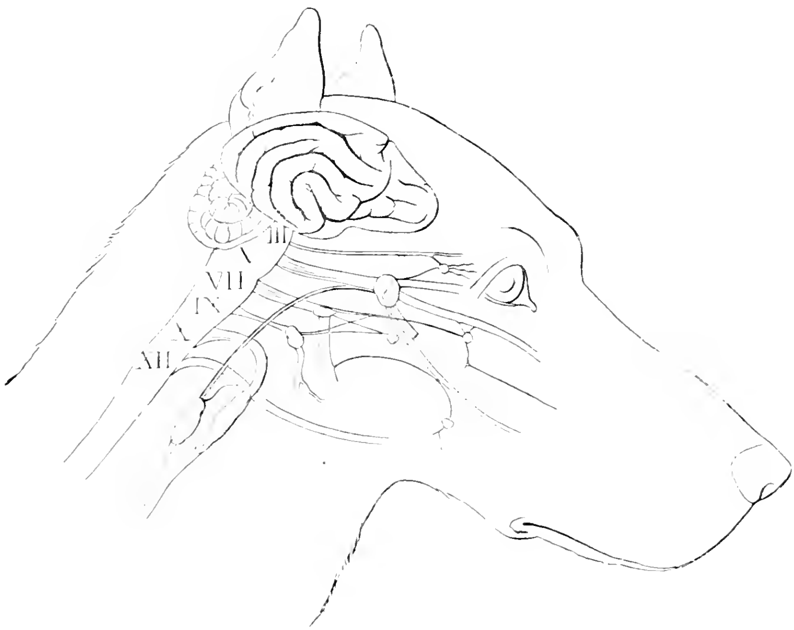


FIG. 68.—Diagram representing the principal cranial nerves and their chief anastomoses by means of their ganglia, in the dog.

III, oculo-motor; V, trigeminal; VII, facial; IX, glosso-pharyngeal; X, pneumogastric; XII, hypoglossal.

The great sympathetic forms a common trunk (vago-sympathetic) with the pneumogastric in the neck, and becomes distinct before throwing itself into the superior cervical ganglion. In the skull, the sympathetic chain is represented by a branch proceeding from the superior cervical ganglion to the ganglion of Gasser, and from thence to the ophthalmic spheno-palatine and otic ganglia of the trigeminal.

The trifacial pair, which may be looked upon as condensed, when its roots and its Gasserien ganglion (the equivalent of a spinal ganglion) are taken into consideration, is, on the contrary, found to be dissociated, when its sympathetic ganglia are regarded.

Cranial sympathetic.—The three first of these ganglia are attached to the chain of the great sympathetic by a double branch, which,

leaving the superior cervical ganglion, proceeds to join them; one of these branches forms the carotid plexus and goes to seek them separately; the other (and it is this which I consider to form *the cranial prolongation of the cervical cord*) terminates in the Gasserien ganglion, is distributed to the three branches of the trigeminal, and by the intermediation of these latter comes into relationship with the three ganglia (ophthalmic, spheno-palatine, and otic). The reality of these connexions is shown by experiment: excitations applied to the cervical cord pass through these ganglia in order to dilate the pupil, to cause certain glands to secrete, and to act on the circulation of certain areas of the face.

Branches of distribution and branches of origin of the sympathetic in the skull.—Like the spinal pairs, the trigeminal receives elements from the great sympathetic, which are intermixed with its branches of distribution and proceed to the apparatus whose function it presides over (vessels, glands, involuntary muscles); but, like the spinal pairs, it supplies in its turn original branches to the ganglia which correspond to it, and this is proved by experiment: the stimulation of the origins of the trigeminal in the skull has the same effect as that of the cervical sympathetic; it reacts on the pupil, on certain vessels, and on certain glands.

Connexions with the oculo-motor nerves.—The motor nerves of the eye are also connected with the great sympathetic; from it they receive slender branches which are destined for the vessels of the muscles which they supply; further, by means of the oculo-motor, they give to it more than they receive from it, because it is through it that the thick and short branch is furnished which is one of the roots of the ophthalmic ganglion, and which represents the *constrictor nerve of the pupil.* The long and slender branch which is supplied by the ophthalmic division is its dilator nerve.

Connexions with the hypoglossal.—At the other extremity of the medulla oblongata the connexions of the hypoglossal are established with the superior cervical ganglion, which supplies it with a very obvious anastomosis and one whose function is well defined (constrictor nerve of the vessels of the tongue). On the other hand, the hypoglossal supplies few or no original elements to the great sympathetic (experiment does not reveal their presence).

Ganglionic elements of the facial.—In the interval which separates the hypoglossal from the trifacial pair, the relations of the great sympathetic with the facial, the glosso-pharyngeal and the pneumospinal nerves, appear to be altogether interrupted. Yet these relations exist, but in order to demonstrate them, it is once again necessary

to resort to experiment. The facial sends to three of the ganglia of the trigeminal three important branches: the two superficial petrosal nerves (large and small) for the spheno-palatine and otic ganglia, and the chorda tympani for the submaxillary ganglion. It is obvious that these branches act on the vessels (dilatory nerves) and on the glands (secretory nerves) of the corresponding localities. They are then origins of the great sympathetic, which must be added to those referred to above.

Geniculate ganglion: its nature.—It is usually considered that these three branches arise from the nerve of Wrisberg through the intermediation of the geniculate ganglion. The question to be determined is if this ganglion is purely sensory, or whether it is mixed in function. Even for the ganglia of the posterior roots, this question is not absolutely settled. According to Onodi, the ganglia of the great sympathetic and the spinal ganglia take origin in immediate proximity the one to the other, and are only separated afterwards; is it possible that a portion of the first remains incorporated in the mass of the second? This question may be propounded, but it has not been answered.

Ganglion of Andersch: Jugular and Plexiform Ganglia.—The glosso-pharyngeal and the pneumogastric nerves pass through ganglia, to which may confidently be attributed the sensory nature of the spinal ganglia; but, it being admitted that these two nerves have important vaso-motor and secretory functions, and that they possess these functions from their origin, it is probable that these ganglia are also mixed, that is to say, half sensory like the spinal ganglia, half motor of the vegetative life, like those of the great sympathetic.

1. Nerves of Special Sense

Those organs, and therefore those nerves, are called *sensorial*, which subserve the special senses other than the tactile sensibility, known as general. This convention might lead to the supposition that the tactile sense is only an element common to the other senses, which represent it merely in a differentiated condition. As a matter of fact, touch, properly so called, is itself a sensation differentiated in a special direction. That which earns it the name of general sensibility is not its more simple physiological modification, but its more extensive anatomical distribution. Just as the other senses, it also presents numerous gradations.

Amongst the nerves of special sense, or sensorial nerves, there are some which in the medulla oblongata really reproduce the arrangement of a posterior root; such are the glosso-pharyngeal and the

auditory, which have nuclei of origin analogous to those of the trigeminal, itself the bulbar nerve of touch; but there are others, such as the olfactory and especially the optic, whose morphology has entirely broken away from this arrangement of nerve roots. These nerves are in reality tracts of the spinal cord or of the brain prolonged to the neighbourhood of the organs of sense (neurons of projection of the second degree), at the extremity of which grey matter is found (retina), and, arising from the latter, microscopical nerve elements (rods, cones), which represent neurons of the first or peripheral order.

a. Olfactory Nerve

This name must be limited to the collection of nerve filaments which creep in the pituitary mucous membrane, and are prolonged to the

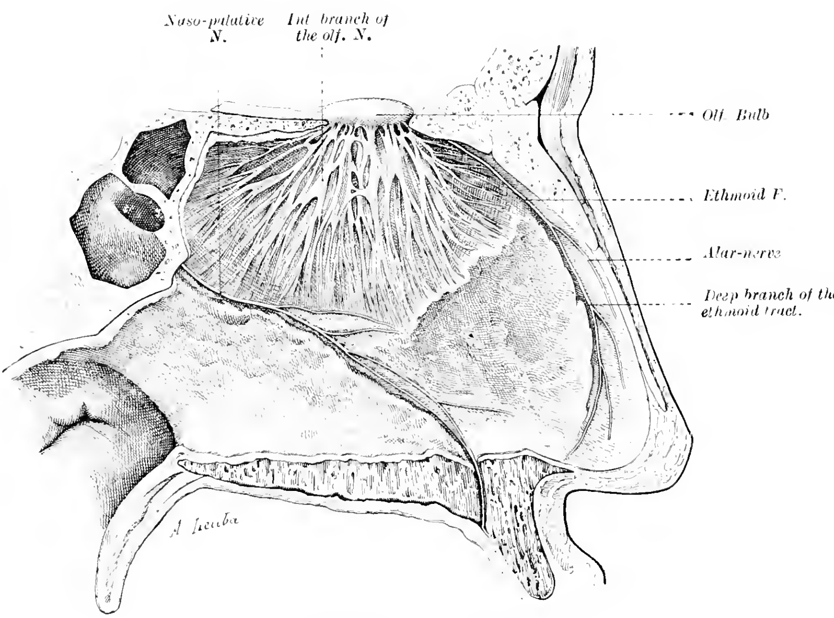


FIG. 69.—Branches of the olfactory nerve.

This figure only shows the branches which are distributed to the internal surface of the nasal fossa (after Hirschfeld).

olfactory bulb, by passing through the perforations of the cribriform plate of the ethmoid. These bundles have no ganglion in their course, but their fibres take origin from cells which have persisted in the olfactory mucous membrane, together with epithelial elements which cover the latter. This is an arrangement which is common to the neurons of special sense, and distinguishes them from the neurons of general sensation. This arrangement is, further, that usually found as regards the nerves of sensation in the invertebrata.

It is allowed without dispute that the olfactory nerve is the conductor of olfactory impressions, and that it is the only conductor thereof. Yet its function has been called in question by Magendie, who believed that the sense of smell was preserved in animals after he had destroyed the olfactory bulb. The sense of smell would then have appertained to the fifth pair, whose filaments are distributed in the nasal mucous membrane, together with those of the olfactory nerve. But the substance which was made use of (ammonia) was an irritating vapour which acted on the terminations of the nerve of touch; and this explains the evidences of disgust which the animals evinced. On the other hand, section of the trigeminal induced, after a certain period, trophic changes in the sensory apparatus to which branches of this nerve are distributed. Hence result secondary sensorial paralyses or pareses, which are the result of a mechanism entirely different from that which causes paralyses or pareses of the sensorial nerve itself, but which may be attributed to the latter if this circumstance is not taken into account.

Cl. Bernard, Le Bec. Testut have ascertained the absence of the olfactory bulb and the olfactory tract (formerly known as the olfactory nerve) in persons in whom the sense of smell was present during life. Le Bec's case has been submitted by M. Duval to histological investigation. This author has ascertained, on the one hand, the presence in the pituitary membrane of olfactory filaments; and, on the other, in the brain, the existence of a real olfactory tract; whence the conclusion follows that the intermediate conductors must have been present, although following an abnormal course.

b. Optic Nerve

Just as the olfactory tract must not be described by the name of olfactory nerve, so the optic nerve should no longer be regarded as being the extended link between the retina and the brain passing through the chiasma, but only the neurons which directly receive the luminous impression and communicate it to the ganglionic elements of the retina. In the limited thickness which separates the retinal surface from these ganglionic cells two superposed layers of neurons may be defined: (1) the rods and the cones, (2) the bipolar cells; and there is a discussion as to whether it is the first or the second which represents the sensory nerve of vision, and which is therefore equivalent to the neurons of the posterior roots in the exercise of the sense of touch. The function of these elements must not be separated from that of the retina, to which we shall several times have to return.

c. Auditory Nerve

The auditory nerve suggests, far more than the preceding forma-

tions, the typical arrangement of an ordinary sensory nerve. It is massed together into a trunk which, from the internal ear, is distributed to the lateral portions of the medulla oblongata, it runs side by side with the facial nerve and the intermediary nerve of Wrisberg in the interosseous portion of its journey through the internal auditory canal. Like the other nerves of special sense, it has nevertheless its cells of origin at the periphery, in the ganglia, included in the interior of the special apparatus of the sense of hearing. In reality this nerve is double, and corresponds to two distinct functions : that of *audition or reception of sounds* by a special apparatus contained in the *cochlea* and that of the reception of special impulses connected with the idea of *movement* or of *position in space* by another equally special apparatus contained in the *semicircular canals.* One is the *cochlear* nerve, the other the *vestibular* nerve ; the cells of origin of the first are situated in the ganglion of Corti or spiral ganglion ; those of the second in the ganglion of Scarpa.

d. Nerves of Taste

The elements of the gustatory special sense are contained, as regards their greater portion (base of the tongue and isthmus of the throat) in the glosso-pharyngeal, and as regards a smaller part (tip of the tongue) in the chorda tympani, a branch of the facial mixed with elements whose functions are diverse. Their experimental study is included in that of the nerve trunks.

2. Sensory and Motor Nerves

In a first natural group are included the motor nerves of the eye, namely : the *oculo-motor* (3rd pair), the *pathetic* (4th pair), the *external oculo-motor* (6th pair) ; then important and complicated nerves like the *trigeminal* (5th pair), the *facial* (7th pair), the *glosso-pharyngeal* (9th pair), the *vagus or pneumogastric* (10th pair), the *spinal accessory* (11th pair), the *hypoglossal* (12th pair). As applied to the cranial nerves, the expression " nerve pair " is devoid of all physiological signification, in the sense of that which is given to it in the case of the spinal nerves (union of a sensory and motor root) ; it simply describes the two nerves which are symmetrically detached from the medulla oblongata at the same level.

a. Oculo-motor

The oculo-motor nerve supplies the levator palpebræ superioris, and in addition four (out of the six) of the muscles of the eyeball, namely, the superior rectus, the internal rectus, the inferior rectus, and the

inferior oblique. Paralysis of this nerve is rendered evident by *external strabismus* (a non-compensated contraction of the external rectus), and a displacement of the eye both downwards and inwards, together with a slight rotation, due to the superior oblique. Downward and upward movements are impossible. The *upper eyelid falls* on account of the predominant action of the orbicularis palpebrarum.

Borrowed sensory elements.—The oculo-motor nerve receives an anastomotic fibre from the ophthalmic branch, which is of sensory function (muscular sense).

Original ganglionic elements.—At its origin this nerve includes the highest root of the great sympathetic. It separates from it in the form of a thick and short filament, which proceeds to the ophthalmic ganglion and thence, by the ciliary nerves, to the muscular apparatus of the iris and to that of accommodation. In addition, therefore, to the movements of the muscles referred to above, stimulation of the oculo-motor causes contraction of the iris and protrusion of the crystalline lens. The antagonistic action (dilatation of the iris and flattening of the crystalline) is effected by the slender branch of the nasal nerve, which originally arises either from the great sympathetic or from the trigeminal itself. The oculo-motor nerve receives ganglionic elements not only through its proper roots, but also by its anastomoses with the chain of the great sympathetic properly so called.

b. External Oculo-motor and Pathetic

The external oculo-motor is distributed to the external rectus muscle; its paralysis causes *internal strabismus*. The pathetic is distributed to the superior oblique; its paralysis is followed by a *deviation of the globe of the eye* upwards and outwards.

The oculo-motor nerve alone of the motor nerves of the globe of the eye appears to supply branches of origin to the cranial ganglia of the great sympathetic, but all receive from this nerve branches of distribution which, without any doubt, are destined for the vessels of the muscles of the eye.

Sensory elements.—All the motor nerves of the eye are, on the other hand, in an anastomotic relation with the ophthalmic branch, as much by recurrence near to their extremities, as directly at the level of the cavernous sinus. These sensory elements are destined for the ocular muscles, *whose degree of contraction they estimate and measure*, so that it may be proportioned to the movement about to be undertaken.

c. Facial

The facial nerve arises from the medulla oblongata by two roots:

the one larger, *motor*; the other very small (*pars intermedia of Wris-*

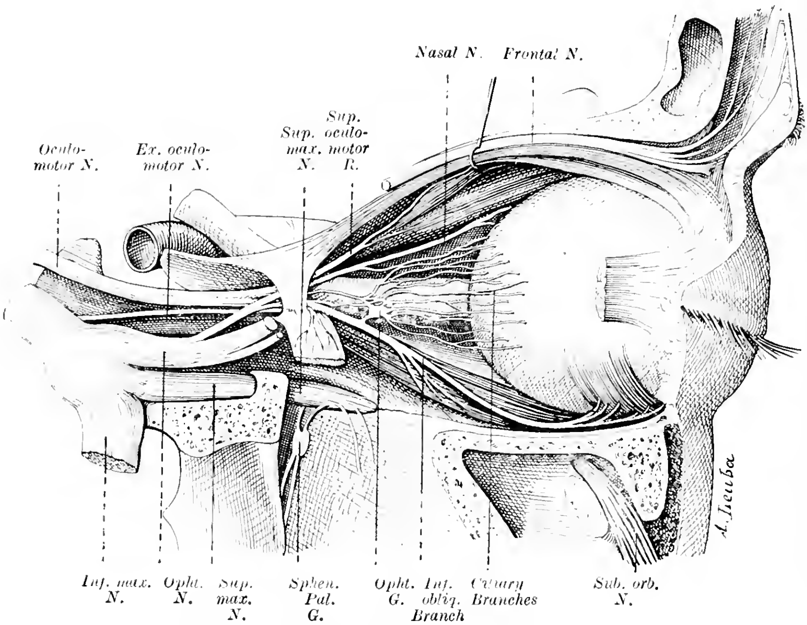


FIG. 70.—Principal nerves of the eye, motor, sensory, sensorial and ganglionic. Their anatomical relations.
Ophthalmic ganglion; direct and indirect ciliary nerves.

berg), terminating in the ganglion (*geniculate ganglion*), situated on one of the angles of the nerve in its transit through the intrapetrous

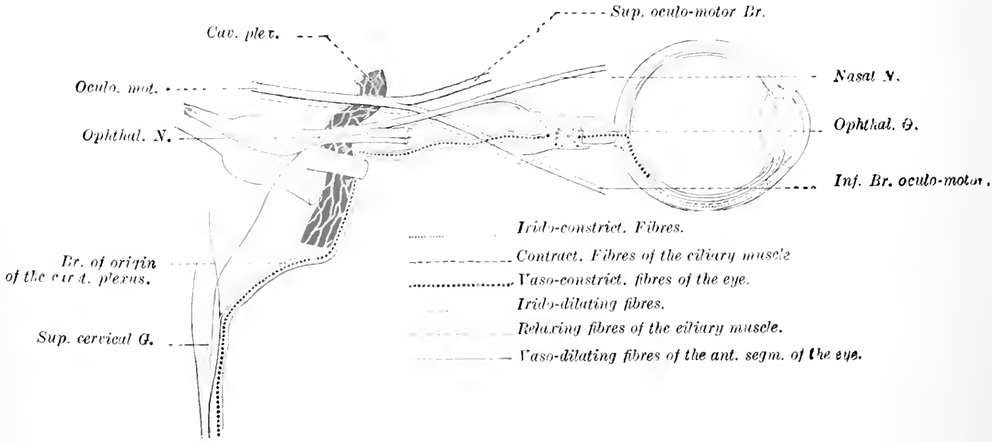


FIG. 71.—Constitution of the ophthalmic ganglion (diagram after Cunéo).

portion of the temporal bone, and which would appear to be sensory.

The facial has, further, vegetative sensori-motor functions resembling those of the great sympathetic; this nerve was the *small sympathetic* of older observers.

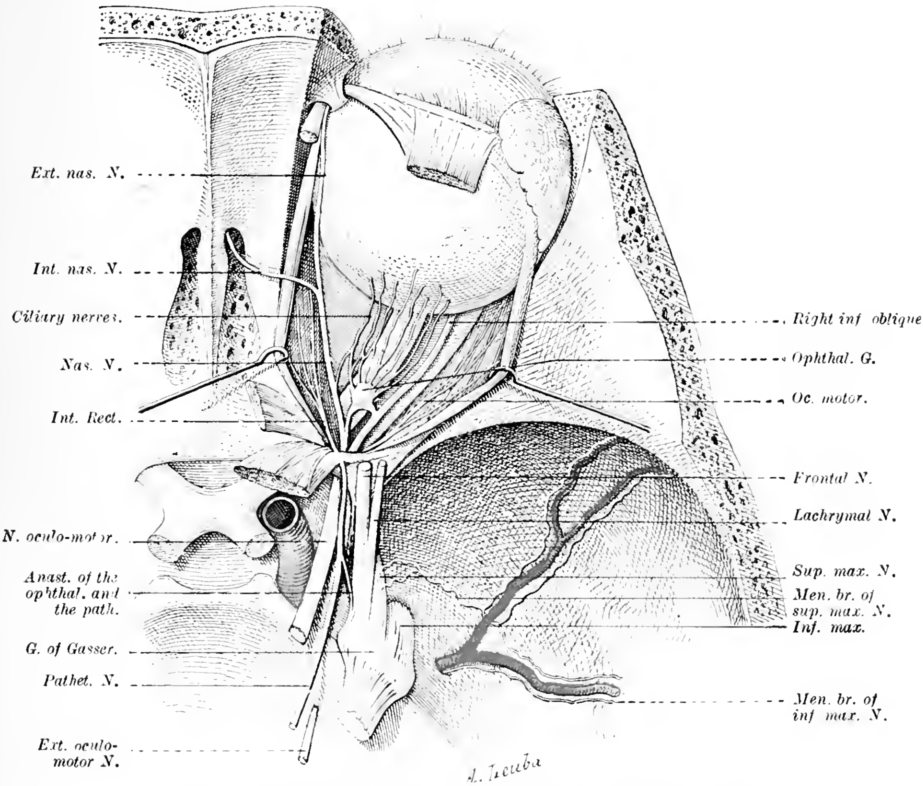


FIG. 72.—Principal nerves of the eye and their anastomoses.

More especially, branches of the superior maxillary branch of the trigeminal proceeding to the dura mater.

Intracranial Section.—The facial nerve may be cut in several ways; the following method is preferable: an incision is made behind the ear and the space between the condyle and the superior curved line of the occipital bone is laid bare. Then the occipital bone is perforated, being very thin in this locality. The neurotome slides along the petrous portion to the internal auditory meatus, where the nerve is cut (necessarily also the auditory nerve).

Intracranial section of the nerve thus effected reproduces the symptoms of paralysis, at the same time *peripheral and deep*, of the facial nerve.

A. PERIPHERAL PORTION.—The paralysis known as *peripheral* is that which involves the muscles of the face when the section of the nerve is effected (experimentally or pathologically) at its exit from the skull at the stylo-mastoid foramen. These muscles, inserted by

one of their extremities in the skin of the face, produce in the latter, or disturb in it, certain folds, and give to the physiognomy that

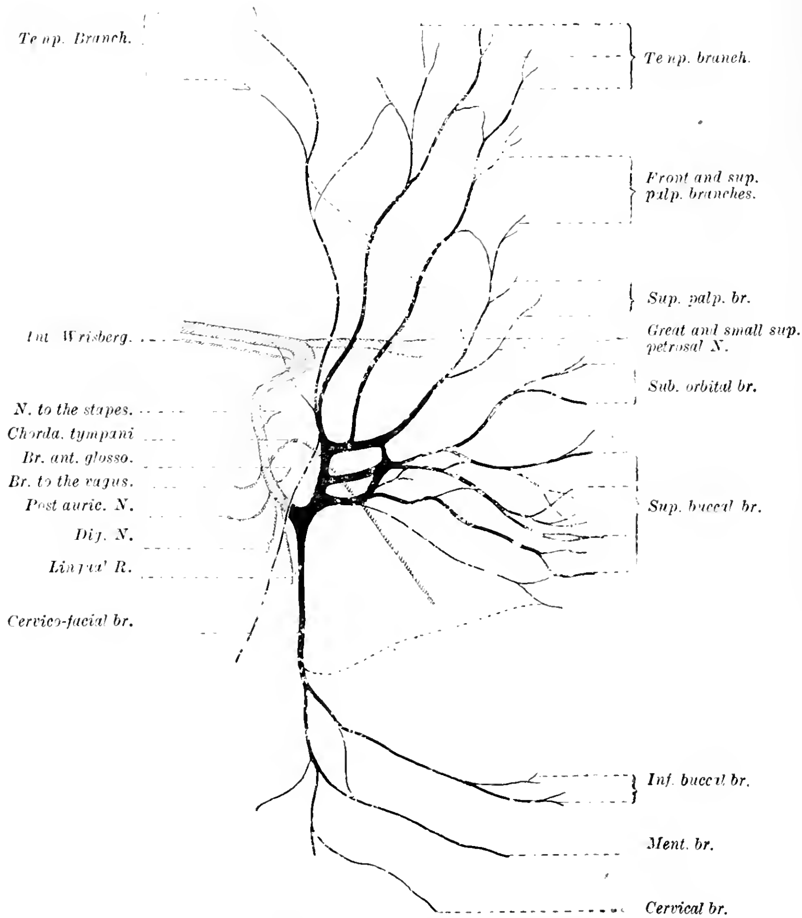


FIG. 73.—Diagram of the facial (after Cunéo).
The terminal branches are in black, the collateral branches in grey.

particular expression which externally displays each of our emotions. Hence the facial is known as the *nerve of expression.*

In addition to these distinctive or *emotional functions,* there are other *voluntary* functions, as we can easily prove on ourselves ; there are also purely *reflex* or automatic functions, such as the closure of the eyelids which is effected by the orbicularis on the threatened entrance of a foreign body, the dilatation of the nostrils which accompanies each inspiration, the movements of the lips which accompany mastication.

1. **Deviation of the features.**—In unilateral paralysis, the loss of

muscular tone on the side corresponding to the paralysis causes a drawing over to the opposite side by the non-paralysed muscles. Owing to the paralysis of the orbicularis, the eye remains wide open. Paralysis of the buccinator muscle causes the cheek to be distended at each expiration, which is expressed by the saying that the patient is smoking a pipe (*fume le pipe*). The ear, but only in animals, drops, in consequence of the weakness of some of the external muscles.

When the paralysis is bilateral, the face resembles a mask.

2. **Elements of general sensation: sensation by recurrence and by anastomosis.**—The peripheral portion of the facial contains elements of general sensation. If, after having cut this nerve at its exit from the stylo-mastoid foramen, its peripheral and central ends are successively pinched, it will be noticed that both are sensitive; the first by *recurrence* of the fibres of the trigeminal, which form plexuses with the terminal branches of the facial; the second by *anastomosis* of the branch arising from the jugular fossa (auricular branch or nerve of Arnold) of the pneumogastric, which thus supplies some sensory fibres to the facial nerve (Cl. Bernard).

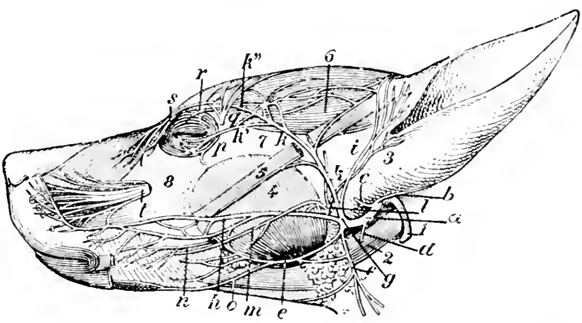


FIG. 74.—Superficial nerves of the head in the dog (after Ellenberger and Baum).

a, facial; *b*, posterior auricular; *c*, internal auricular; *d*, branch of the digastric; *e*, inferior buccal; *f*, superior transverse cervical; *g*, zygomatico-temporal branch of the facial; *h*, superior buccal; *i*, its temporal branch; *k*, its zygomatic branch; *k'*, its branch for the lower eyelid; *k''*, for the upper eyelid; *l*, superficial temporal; m, malar or parotid branch; *n*, buccinator; *o*, branch of the mylo-hyoid; *p*, orbital branch of the superior maxillary; *q*, lachrymal; *r*, frontal; *s*, subtrochlear; *t*, sub-orbital.

1, styloid apophysis; 2, digastric; 3, pinna of the ear; 4, masseter; 5, large zygomatic; 6, scutellar; 7, zygomatic arch 8, superior maxillary.

B. DEEP PORTION.—The *deep* portion of the facial is represented by branches which it supplies in its transit through the petrous portion. or immediately on its exit from this bone.

1. **Motor Elements.**—As regards the *motor* function, paralysis of these branches (the result of intra-cranial section of the nerve) is rendered evident by *a difficulty of swallowing*, by a nasal tone of voice and by a deviation of the uvula to the side opposite to that paralysed. The difficulty of swallowing is due to the paralysis of the digastric, and of the stylo-hyoideus, and also of the palato-glossus and of the

palato-pharyngeus, the nasal tone of the voice to that of the levator palati; the deviation of the uvula to that of the azygos uvulæ.

The fibres which proceed to the soft palate and to its pillars are conducted thither by the posterior palatine nerves, which proceed from the geniculate ganglion by the intermediation of the large superficial petrosal nerve, and of the spheno-palatine ganglion. It is a question whether these nerves are not closely united to these ganglia, or whether, as Longet holds, they actually form a component part of them. The exact origin of the motor nerves of the soft palate is not clearly known.

2. **Sensory elements.**—The soft palate receives for its pillars some sensory gustatory elements which come to it through the palatine branch of the nerve of Wrisberg (Vulpian).

3. **Ganglionic elements: superficial petrosal nerves.**—The facial contains a notable proportion of nerves, really ganglionic (vegetative in function), which it derives from its own origins (small root, nerve of Wrisberg). The same palatine nerve, which has just been considered, like *the great superficial petrosal nerve* which gives rise to it, contains secretory elements destined for the glands of the mucous membrane of the soft palate; it also contains vaso-dilator fibres for the same structure. The vaso-constrictor fibres are distributed to it by the filament of the great sympathetic, which is closely united to the large petrosal in order to form the Vidian nerve. The *small superficial petrosal*, which from the facial proceeds to the otic ganglion, is, as regards its function, but imperfectly known.

Deep petrosal nerves.—The great and small superficial petrosal nerves each receives from the glosso-pharyngeal, by Jacobson's branch, an anastomotic branch, which is, as regards the first, the small internal deep petrosal and, as regards the second, the small external deep petrosal. The function of the first is but little known; the second contains secretory and vaso-dilator elements of the parotid gland. Leaving the glosso-pharyngeal, they then follow a branch of the facial; having passed through the otic ganglion, they enter the auriculo-temporal branch of the inferior maxillary and then pass into the parotid. Thus the glosso-pharyngeal and the facial both take part in the vaso-motor and secretory innervation of the salivary glands and of the soft palate. This is proved by stimulating these two nerves at their cranial origin (Vulpian).

Branch to the muscle of the stapes.—The facial supplies a small branch which proceeds in the middle ear to the muscle of the stapes. Its action is antagonistic to that of the filament to the internal muscle of the malleus, which takes origin in the trigeminal; it relaxes the membrana tympani and lowers pressure in the labyrinth.

Chorda tympani.—An anastomotic branch extends from the facial

to the lingual and skirts the internal surface of the membrana tympani ; for this reason it is known as the chorda tympani. Distributed to the tongue, to the sub-maxillary and to the sub-lingual glands, this branch is *vaso-dilator* as regards these three organs ; it is *secretory* in function for the two glands. We shall see a little further on that this important branch also contains centripetal elements. With the two superficial petrosal nerves it is regarded as the principal continuation of the small root, or nerve of Wrisberg.

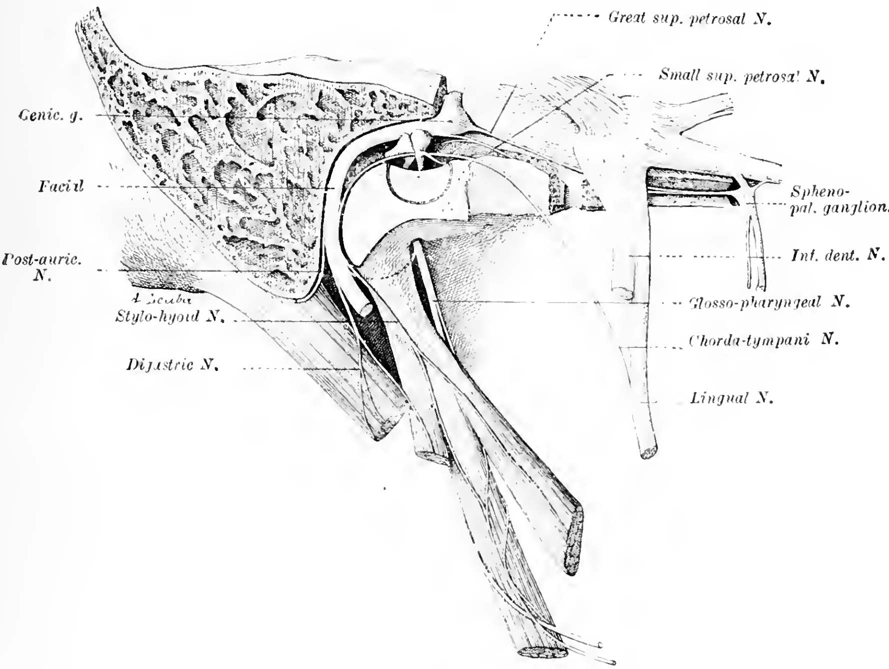


FIG. 75.—Deep branches of the facial.

More especially the chorda tympani : the superficial petrosal nerves, the branches of the styloid muscles and their anastomosis with the glosso-pharyngeal.

C. ORIGINS.—This analysis, which is effected as we ascend from the periphery to the centre, leads us to the origins of the facial nerve, these being formed by the trunk, properly so-called, of the seventh pair, or the larger root, and the nerve of Wrisberg, or the smaller root.

Intra-cranial excitation. The isolated stimulation of the two roots of the facial (even after the skull has been opened) is not easily effected. But at least we may inquire if in either of the elements general sensation be present. Cl. Bernard denies this, basing his opinion on the fact that this stimulation was painless, while the root of the trigeminal of the same animal was very sensitive.

Hence the elements of ordinary sensation will be present in very small number. On the other hand, this stimulation brings into action, tolerably easily, the voluntary and involuntary motor elements which have been considered above.

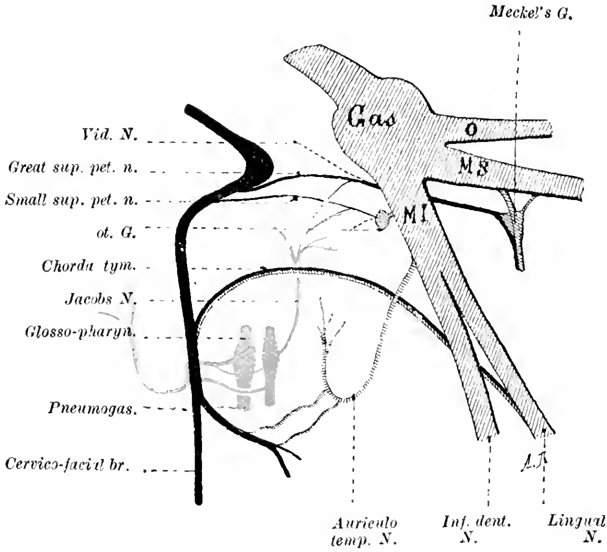


FIG. 76.—Diagram of the anastomoses of the facial with the trigeminal, the glosso-pharyngeal, and the pneumogastric. Superficial and deep petrosal nerves.

The colours do not represent functions, but merely anatomical nervous groups.

Gustatory Sense.—The opinion which has prevailed concerning the function of the small root of the facial or nerve of Wrisberg is, that it represents an aberrant origin of the glosso-pharyngeal nerve, which is destined for the tip of the tongue by the path of the chorda tympani, and for the soft palate by the large superficial petrosal nerve and the posterior palatine nerve, which is one of its branches of continuation. Its bulbar nucleus appears, indeed, to continue the nucleus of the ninth pair above and in front (M. Duval, Vulpian).

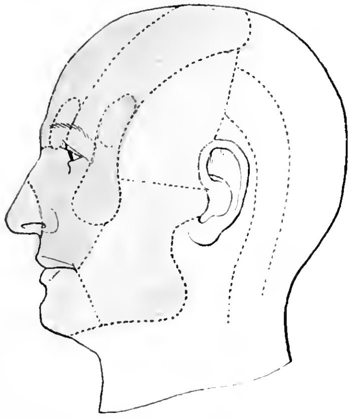


FIG. 77.—Sensory areas of the branches of the trigeminal.

The area of the ophthalmic in red; that of the superior maxillary in yellow; that o the inferior maxillary in blue.

Intracranial paralysis of the facial and section of the chorda tympani are accompanied with *a marked diminution of taste at the tip of the tongue and of the pillars of the soft palate.*

Secretory and Vaso-dilatory Action.—As regards movement, intracranial stimulation of the facial, besides the contraction of the muscles of the face, of the digastric, of the stylohyoid of the tensor palati, of the azygos uvulæ muscle, etc., induces secretion of the sub-maxillary and sub-lingual glands,

as also of those of the soft palate; it causes congestion of these same organs and of the mucous membrane of the tongue and of the soft palate.

Indirect action on several senses.—Thus the facial is directly connected with the sense of taste, at least as regards the tip of the tongue and the soft palate.

But its paralysis may also induce, in a roundabout way, disorders of the other senses. The eye is deprived of its protective winking of the eyelid: nevertheless it does not become inflamed as it does after section of the trigeminal. One of the muscles of the middle ear is paralysed. The sense of smell is itself embarrassed by the absence of dilatation of the nostrils and by paralysis of the palate (Longet).

Mixed nature of the geniculate ganglion and of the nerve of Wrisberg.—The geniculate ganglion has been sometimes described as a ganglion of the great sympathetic, sometimes as a spinal ganglion, and those who hold one of these opinions reject the other: they are not, however, incompatible, and it is probable that the nerve of Wrisberg contains both vegetative elements and those which are sensitive, or rather, sensorial, as is the case with the posterior spinal roots

d. Trigeminal.

The sensory distribution of the trigeminal corresponds to the whole of the *face* (including the forehead), as also the corresponding cavities (this distribution is that of its *sensory* or ganglionic root). It causes contraction of the masseter, temporal, internal and external pterygoid and mylo-hyoid muscles, which take an essential part in the act of mastication (this function appertains to its small root, *motor* root, masticatory root of Bellingeri).

Intracranial section of the trigeminal.—Intracranial section of the trigeminal, the animal surviving, was first performed by Magendie, and it has become one of the classical operations of neurology. It is easily performed in the rabbit, in which the cranial walls are thin, and may be effected also in the dog. The neurotome made use of has a fine blade ending in a triangle, which is adapted both for pricking and cutting: with this the cranial wall is perforated in the middle temporal fossa immediately behind the condyloid tubercle of the lower jaw. When the instrument is once in the skull it is directed against the anterior face of the petrous portion of the temporal bone, at the point where the depression in which the trigeminal with its ganglion is situated. The instrument is then turned downwards, and is at the same time withdrawn in order to catch the nerve and to cut it by the steel triangle in which the neurotome ends. At this instant the animal utters cries, and the eyeball protrudes.

A. Sensory and motor functions.—Anatomically considered, the trigeminal has the constitution of a spinal pair: this view is verified in every way by experiment.

Sensory paralysis.—After section of the fifth pair, it is found that the cornea, the conjunctiva, the tongue, the skin of the face, and the mucous membranes of these cavities are insensible on the side operated on, except as regards their deeper portion where the distribution of the trigeminal is mingled with that of other nerves. The ear remains

sensitive on account of the important branches which it receives, both from the cervical plexus and the pneumogastric.

Borrowed sensorial element.—Isolated section of the lingual nerve causes the disappearance in the tip of the tongue both of general sensation and of the sense of taste. But while the tactile elements of this area arise from the origins of the trigeminal, its gustatory elements are supplied to it by the nerve of Wrisberg by the aid of the facial and of the chorda tympani.

Motor paralysis.—If both trigeminals are divided, *mastication* becomes *impossible.* If the section is unilateral, inasmuch as the

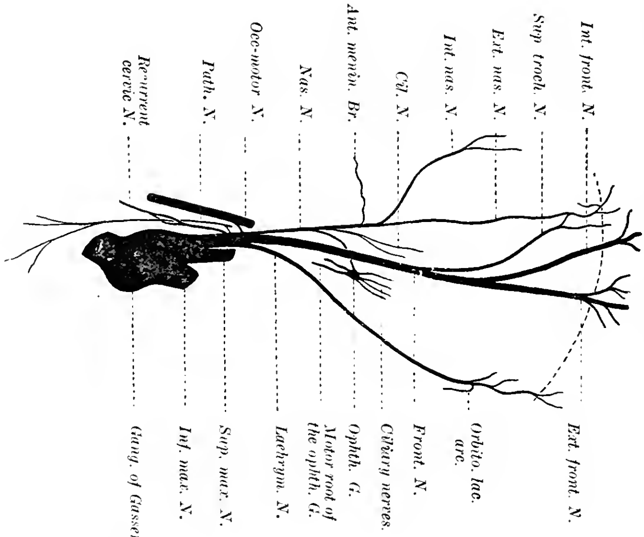


FIG. 78.—Diagram of the ophthalmic nerve and of its branches.

two halves of the lower jaw form a consolidated whole, mastication may still be partially effected by means of the muscles of the intact side ; but the jaw is *deviated* and drawn to the sound side ; the teeth no longer correspond ; one incisor of the upper jaw opposes a single incisor of the lower ; the two others, being no longer kept in place by mutual opposition and regular use, grow unduly long.

Intracranial excitation.—If the roots of the trigeminal in the skull be exposed, direct excitation will show that the *large root is endowed with acute sensibility, while the small root is motor for the muscles of the jaw* (masseter, temporal, internal and external pterygoid, and mylohyoid).

B. CONNEXIONS WITH THE GREAT SYMPATHETIC.—Like all the nerve trunks proceeding from the spinal cord or the medulla oblongata, *the trigeminal contains elements originating in the great sympathetic, and*

receives branches of distribution from this nerve. These sensori-motor elements (of sub-conscious sensation and of involuntary movement) fulfil very diverse functions, all of which relate to the connexions between organs, and which on this account have a bearing on nutrition.

Secretory elements.—To speak here only of the secretory elements, the trigeminal supplies these to the lachrymal gland, to the sudoriparous glands of the face, and to the eye itself for the regulation of its internal tension; they proceed to it either from the cranial sympathetic, or from its own origins. It furnishes secretory elements to the glands of the velum palati and to the submaxillary and sublingual glands,

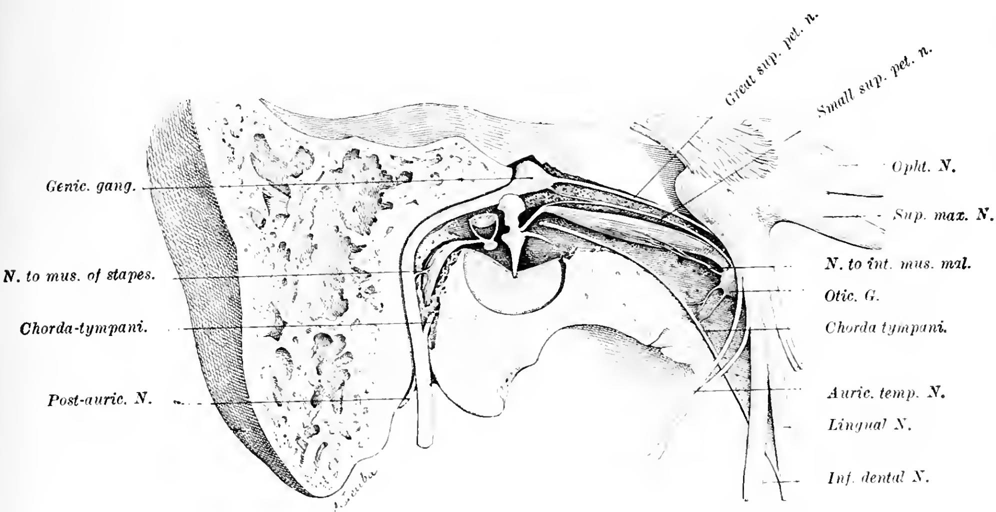


FIG. 79.—Innervation of the muscles of the ossicles and chorda tympani.

Internal muscle of the malleus receiving a branch of the trigeminal nerve through the otic ganglion. Muscle of the stapes receiving a branch of the facial.

which come to it from the nerve of Wrisberg. It supplies the same to the parotid and the molar gland, the so-called gland of Nück, which proceeds to it from the glosso-pharyngeal, without its origins or the cranial sympathetic taking any part. But the nerve of Wrisberg and the glosso-pharyngeal take some part, like the pneumogastric, in the formation of the ganglionic system. The vaso-dilator elements of the same organs have the same origin. Generally speaking, the constrictors are supplied from the cervical sympathetic.

C. TROPHIC DISTURBANCES.—Intracranial section of the trigeminal reacts in different ways on the nutrition of the face in a more or less direct or indirect manner. Magendie observed that, after section of

this nerve, the eye loses its brilliancy and its polish. The change, which is visible some hours only after the operation, usually commences in the centre of the cornea in the form of a spot which progressively becomes more and more opaque. At the same time a kind of cloud appears in the anterior chamber. And after some days an invasion of the cornea by a vascular network, which starts from its edge and stops abruptly at a certain distance from its centre, may be seen. In the case of weak or badly nourished animals, destruction of the eye may ensue through perforation of the cornea and escape of the crystalline lens and of the humours (Cl. Bernard). In certain cases Magendie observed the gangrene to extend to the whole of the face.

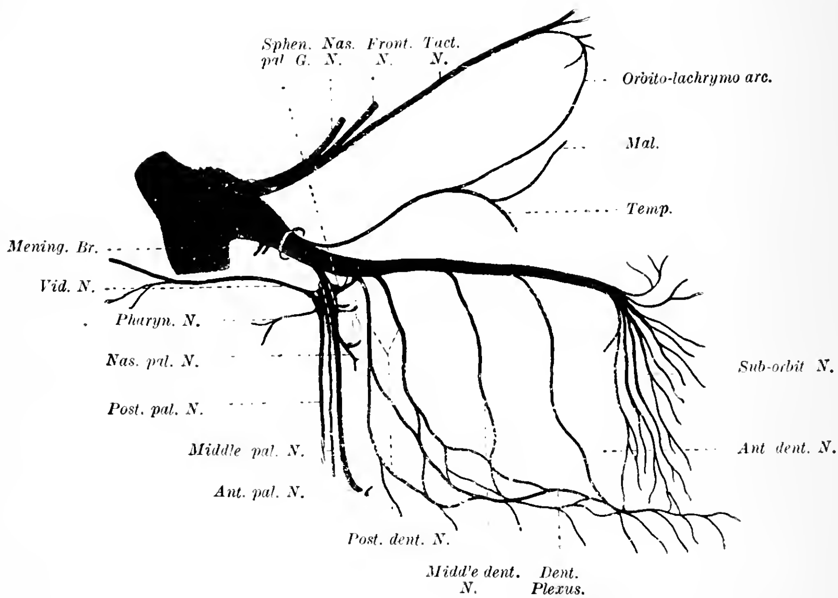


FIG. 80.—Diagram of the superior maxillary nerve and its branches.

Their contingency.—In man, trophic disturbances of the eye analogous to those which have been described, though less severe, have been several times observed to ensue after lesions of the trigeminal nerve. However, these troubles do not appear of necessity, and, especially in surgical intracranial section, they have been moderated or avoided. It must not be forgotten, horweve, that the vulnerability of the parts deprived of their nerve supply is increased, and that these disturbances may thus appear under the influence of ordinary and sometimes slight causes.

Different locality.—Magendie, Cl. Bernard, all those who consecu-

tively to them have performed intracranial section of the trigeminal nerve on animals, have often observed *ulceration* of the upper and lower lip and changes in the conjunctiva, as also in the naso-buccal mucous membrane, affecting the vascularization and secretion of these surfaces.

Photophobia.—When the eye is inflamed, especially the iris and the cornea, a particularly painful sensitiveness to light arises, which compels the patient to avoid luminous rays by closing the eyelid. Although light is the irritant, the origin of this painful sensation does not lie in the retina. Photophobia, indeed, may occur in amaurosis, in which the visual sense no longer exists. When, in animals, the optic nerve has been previously cut, a wound of the cornea induces photophobia (Cl. Bernard, Castorani). Photophobia does not occur when the conjunctiva is alone inflamed.

The iris seems to possess a special sensitiveness to light, and can contract directly under the influence of luminous rays (Brown-Séquard). The sensitiveness of the cornea is supplied by the ciliary nerves known as indirect, which pass through the ophthalmic ganglion ; that of the iris by both the direct and indirect ciliary nerves (Cl. Bernard).

Ophthalmic ganglion : its nature.—Certain authors have discussed the question whether the ophthalmic ganglion (which some call also ciliary ganglion) is the equivalent of a sympathetic or of a spinal ganglion. It is probable that its sympathetic functions, very definitely elicited by experiment, are not exclusive of conscious sensory functions, of the kind of those possessed by the ganglionic root of the trigeminal, of which it would represent an aberrant mass of very small dimensions.

In man, a complete sensory paralysis of the trigeminal, with the exception of the cornea, has been observed ; this would be explained by an alteration of the nerve not involving the ophthalmic ganglion (Thesis of Demaux, 1843).

Classification of the elements.—In all these complicated nerve trunks forming the cranial nerves, experiment demonstrates the existence of three orders of elements : some *sensory* or of special sense, others *motor*, others which are known as *ganglionic* or of the great sympathetic. Fundamentally, these latter are also sensory and motor elements, but of a special order ; they have a double anatomical and physiological character. The neurons which compose them, instead of proceeding from a single point of the spinal cord to the organs, are interrupted in their course by the grey matter of the ganglia ; and, on the other hand, their sensitiveness is obscure and their motor power automatic, that is to say, involuntary.

The different disturbances mentioned above agree with those of the

elements of diverse functions originally contained in the trigeminal, or yielded to its branches of distribution by the anastomoses which come to it from the great sympathetic : vaso-motor elements, secretory elements, together with other elements whose nature is but ill-determined.

Vaso-motor elements.—The trigeminal contains vaso-motor elements supplied to it by the great sympathetic and whose origins are in the second, third, fourth and fifth roots of the dorsal spinal cord. Some of these elements are of constrictive and others of dilatory function as regards the vessels of the face (Dastre and Morat). They are unequally distributed in its different regions or cavities (see *Great Sympathetic*).

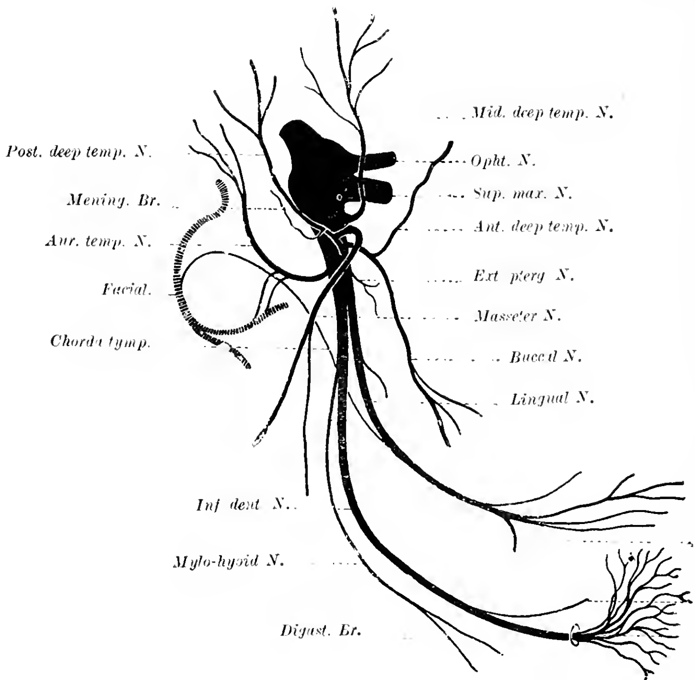


FIG. 81.—Diagram of the inferior maxillary nerve.

They regain the trunk of the fifth pair by passing chiefly by the anastomosis which, from the superior cervical ganglion, proceeds to the Gasserien ganglion. A section made, either through this last ganglion, or in front of it, interrupts the continuity of these elements and explains the vascular disorders which are the consequence of this section in the deep and superficial portions of the eye, as also in the nasal mucous membrane and, in a lesser degree, the mucous membrane of the mouth.

(a) *Constrictor elements.*—The great sympathetic supplies constrictor

elements, both to the branches and to the trunk of the trigeminal. The retina, the bucco-facial region receives branches from it through the anastomosis, which proceeds from the superior cervical ganglion to the Gasserien ganglion. The anterior segment of the eye seems to receive them by a route which is independent of this anastomosis (Morat and Doyon).

(b) *Dilator elements.*—The cranial prolongation of the great sympathetic, which proceeds from the superior cervical ganglion to the Gasserien ganglion, contains the larger portion of the dilators supplied by the great sympathetic to the trigeminal (Morat).

Elements whose function is undetermined.—The trophic disturbances of the

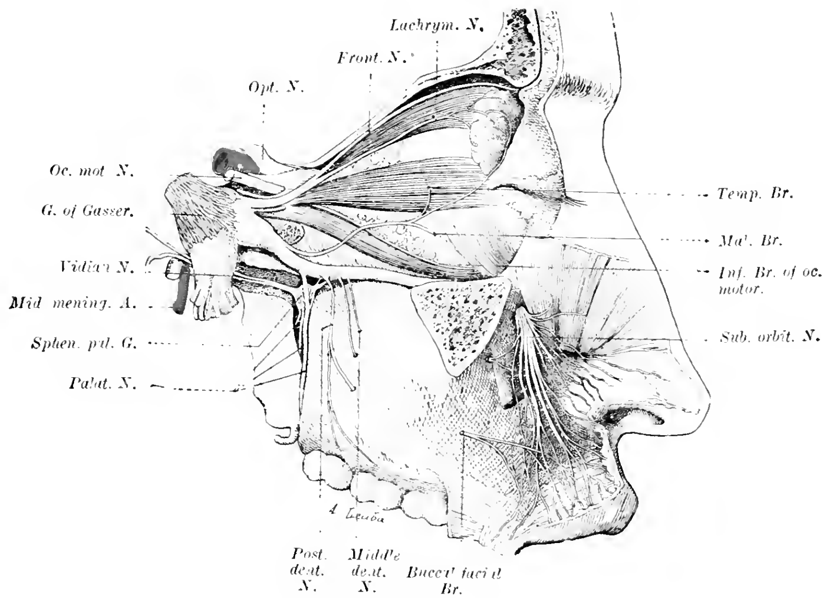


FIG. 82.—Superior maxillary nerve : its superficial branches.

eye and of the face which ensue consecutively to the section or paralysis of these nerve trunks are not satisfactorily explained either by the fact that sensation is abolished, or by the circumstance that the circulation has been disturbed, or even because these parallel alterations of sensibility and of blood supply occur concurrently. Many authors have considered this a proof that there must be in the nervous system particular elements, regulating in a specific manner the cellular nutrition, and which, for this reason, they call *trophic nerves.*

Position of the question.—Presented in this manner, the question is not well propounded, and it is necessary to recast it in its proper aspect. That cellular activity is dominated by the nervous system is a fact which is perfectly clear and incontestable ; but this activity presents itself under diverse aspects ; it is resolvable into multiple phenomena having between them bonds of dependence. We assert in principle that *the nervous system does not intervene in a separate*

manner as regards each of these phenomena by distinct elements, but that it merely supplies to the cell that initial impulsion which causes them to display themselves in the order which is imposed upon them by their serial arrangement.

Typical example.—As a definite example, we may take a muscle. When the nerve of this organ is stimulated it manifests: (1) an elimination of heat, (2) apparent movement, (3) interchanges of its substance with the blood which passes through it. The bond of union between all these internal and external phenomena is in itself so evident that we do not attribute them to three orders of nerves, which would be distinguished according to each one of these special phenomena, but to a single order of fibres which we call motor, in accordance with the most obvious phenomenon and that longest known, which results from their stimulation. These phenomena, in their totality, are often massed together under the name of *nutrition*, which implies an exchange of substance and of energy with the medium which makes good the waste due to muscular work.

Degeneration.—It must be added that it is not a matter of indifference whether a muscle receives stimulations or is deprived of them, whether it acts normally or is condemned to a definite repose. Absolute privation of stimulation induces an alteration of the composition and of the intimate structure of the muscular cell.

This structural change is known as *degeneration* or *trophic alteration* when it has become marked in the muscle element which has continued too long inactive. The motor nerve which presides over the chemical and molecular phenomena which bring about these consequences is thus at one and the same time, a nerve of movement, a nerve of heat production, a nerve of chemical metabolism, and a nerve of nutrition. Every nerve which has an influence on any one cell, in the sense of arousing it to its specific activity, exerts by this very fact a control over a series of analogous or equivalent phenomena which follow one another in the same order, and of which some are immediate and others remote. On the other hand, these phenomena may not be equally visible; the first (functional phenomena) owing to their very nature, may in certain cases elude our observation, while the latter (structural alterations) are necessarily obvious.

Function which is not visible externally.—This is probably what happens as regards organs, such as the skin and the cornea, whose fixed cells, epithelial or otherwise, have a wholly internal activity which is not manifested in any case by visible movement. Doubtless this activity is controlled by nerves in a manner similar to that of the glands; only the stimulation of these nerves has no directly visible effect; while the definite loss of this activity, consecutive to the suppression of these nerves is shown, after some time, by the alterations which are its usual result.

Conclusion.—*The skin and the cornea possess no other trophic nerves than those which preside over the functional activity of their elements.* The details of this activity elude our actual methods of observation. It can only be said that *the cessation of this activity reveals itself by a structural disorder, the result of the loss of nutritive equilibrium.*

Functional analogies.—If this explanation is admitted, if the existence of centrifugal nerves proceeding to the fixed elements of those tissues which are still considered to be deprived of such an innervation is accepted, their elements should take their place alongside those which terminate in the glandular cells. The epithelia known as those of investment, whose function is certainly not limited to that of mechanical protection, which is the one attributed to it, are just as much entitled as the glands to be excited and directed in their functional activity by impulses distributed by the nervous system. These centrifugal nerves, analogous to the secretory nerves, belong, without any doubt, like the latter, to the ganglionic system.

Section of the posterior roots, trophic disturbances.—Section of the posterior lumbar and sacral roots often induces in the corresponding posterior limb ulcerations, with falling off of the nails and the hair of this region, thickening of the skin with hypertrophy of the metatarsal bones and phalanges. These facts resemble those which follow section of the trigeminal nerve. Like the trigeminal, the posterior roots of this region contain sensory elements, and amongst them centrifugal elements whose vaso-dilator function with regard to the corresponding limb has been demonstrated. But here again the trophic disturbances do not seem to be in constant relationship with the modifications of sensation and of vascularization. Hence here once more the existence of centrifugal elements must be allowed, elements which are no longer destined merely for the vessels, but also for the tissues of the skin, and which also belong to the ganglionic system.

D. Indirect action on the senses.—The trigeminal distributes its ramifications in the four cavities of the face containing the organs of the four important senses : the orbital cavity (vision), the nasal cavity (sense of smell), the cavity of the mouth (taste), the auricular cavity (hearing). All these sensory organs are, as it were, enclosed in a field of general sensation, whose territory belongs to it (the trigeminal). The tactile sense is thus indirectly called upon to render assistance to the complicated functions of the superior senses.

The trigeminal takes part in the exercise of these senses, not only by its sensory elements, but also by the involuntary motor elements which appertain to it, both as regards its origins and its anastomoses with the great sympathetic. Without speaking of the vaso-motor elements which regulate the circulation in all these organs, it takes part in a series of reflexes of adaptation and defence of which the principle may here be mentioned.

a. *Vision.*—The ophthalmic ganglion supplies ciliary nerves to the eye, some of which are constrictors, the others dilators of the pupil ; the first come from the oculo-motor, the second from the trigeminal, which receives them both from the great sympathetic and from its origins. The first act chiefly by increasing the curvature of the lens, and thus by accommodating the eye to near vision ; the second act in the opposite manner, namely, by diminishing the curvature and accommodating it to distant vision (Morat and Doyon).

Intraocular tension is maintained in its normal condition by a kind of equilibrium between the internal secretion of the humours of the eyeball and the depletion of the latter.

b. *Hearing.*—The otic ganglion supplies a filament to the middle ear, which proceeds to the internal muscle of the malleus and regulates the tension of the membrana tympani. At its entrance into the muscle, this branch passes through a small ganglion which is the equivalent of the ciliary plexus.

c. *Smell.*—Secretory elements of the spheno-palatine ganglion regulate the degree of moisture of the nasal mucous membrane.

d. *Taste.*—By its lingual branch, the trigeminal gives off an important branch, the chorda tympani, which controls the secretion of the submaxillary gland, and by it the condition of humidity of the tongue most favourable to the sense of taste. The chorda tympani is a borrowed branch which comes originally from the facial and ends in the sub-maxillary ganglion.

e. Glosso-pharyngeal.

From its origins the glosso-pharyngeal is a mixed nerve ; fibres of

general sensibility, gustatory fibres and motor fibres of all kinds run side by side in it in radicular bundles, in which it would be impossible to separate them experimentally. Yet these fibres, whose functions vary so greatly, have nuclei of origin and of termination which are distinct in the grey bulbar substance.

1. *Section :* **Gustatory paralysis.**—Intracranial section of the glosso-pharyngeal nerve cannot be performed in an isolated manner. Section of the nerve at its exit from the skull abolishes gustatory sensation in the posterior portion of the tongue, that is to say, in all the area situated behind the lingual V. The tip of the tongue receives its sensory fibres from the lingual trunk, but in reality by the inter-

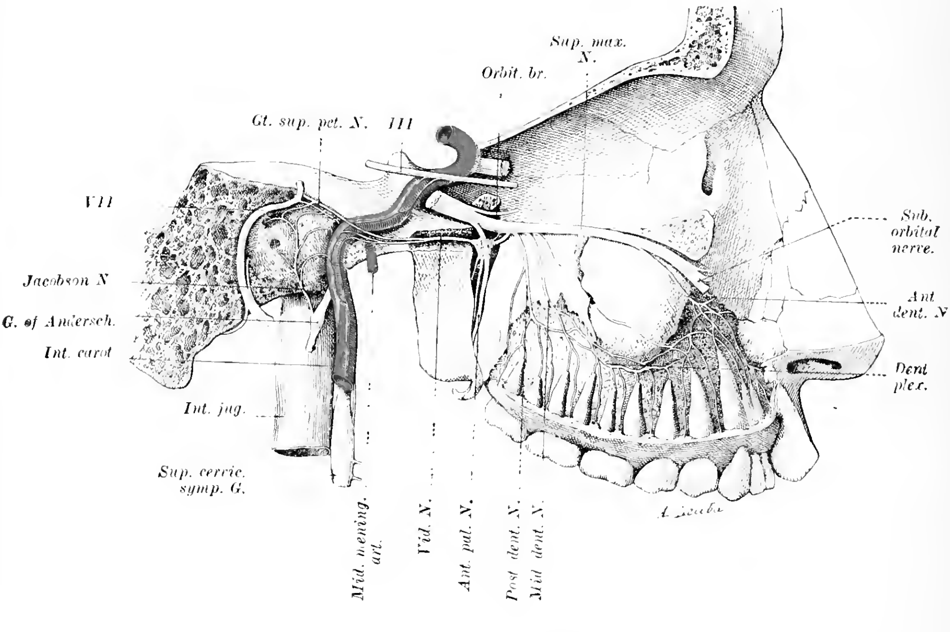


FIG. 83.—Superior maxillary nerve ; its branches and deep anastomoses.

mediation of the chorda tympani, which obtains them from the nerve of Wrisberg.

Sensory paralysis.—Along with its gustatory fibres, the glosso-pharyngeal contains elements of general sensation. Section of the nerve at its exit from the foramen lacerum is painful, and its excitation by pinching is accompanied with cries and defensive movements. The ninth pair presides over general sensibility of the base of the tongue and partly over that of the pharynx, the pharyngeal plexus being made up of elements coming from the glosso-pharyngeal, from the vagus and the great sympathetic.

2. *Stimulation within the skull.*—By the stimulation of its roots within the skull, it can be shown that the glosso-pharyngeal contains motor elements of different categories from its very origin.

Animals are operated on which have just been killed, the animal employed being as large as possible; the motor power in these circumstances persists for a certain time after every kind of sensation is extinct, which allows a sufficient time to elapse in order to study it and eliminates the reflex effects which might be due to sensation. Chauveau has observed in these conditions that stimulation of the roots of the glosso-pharyngeal causes contraction of the *inferior con-*

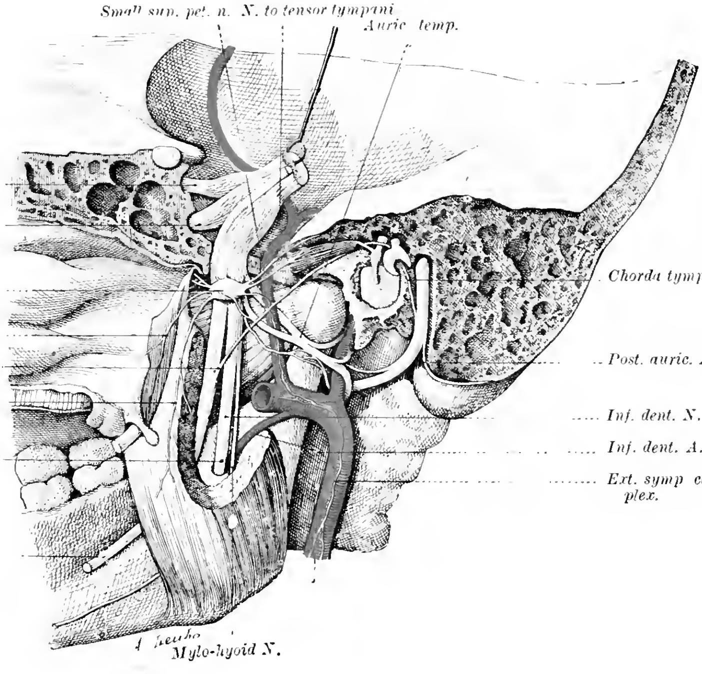


FIG. 84.—Inferior maxillary nerve (internal aspect.)

strictor of the pharynx, and of a portion of the muscles of the soft palate.

Vaso-dilator elements.—Just as the gustatory fibres of the lingual and of the chorda tympani are accompanied by vaso-dilator elements, so also are those of the glosso-pharyngeal. By stimulating without or within the cranium the ninth pair in animals whose circulation is intact, Vulpian has observed a marked *congestion at the base of the tongue* in the area of distribution of this nerve. There is also dilatation of the parotid vessels.

Secretory elements.—The same author has noticed that this stimulation (made within the skull) causes *the parotid glands to secrete.* By combining this result with those previously obtained by Cl. Bernard, Schiff, etc., the course of the secretory nerve of this gland is found to be the following : origin of the glosso-pharyngeal, the ganglion of Andersch, Jacobson's branch, small, deep external petrosal, otic ganglion, auriculo-temporal branch, of which certain ramifications are distributed to the parotid.

Ganglia ; their functional nature.—The same remark may be made concerning the ganglia of the glosso-pharyngeal (ganglion of Ehrenritter and ganglion of Andersch) as concerning those of the greater portion of the cranial nerves ; these ganglionic masses are without doubt the partial equivalent of the spinal ganglia of the posterior roots (sensory and sensorial fibres) ; but it is probable that they also represent the ganglia of the great sympathetic. Jacobson's nerve, which is given off by the ganglion of Andersch, is clearly a nerve of vegetative life, as is shown by its connexions with one of the salivary glands.

f. Pneumogastric

The pneumogastric nerve (still called the *median, sympathetic, vagus* nerve, or nerve of the tenth pair), ramifies in the head, neck, thorax, and the abdomen, that is to say, in numerous and important organs which subserve very varied functions. It includes *sensory* and *motor* elements, both of the *life of relation* and of the *organic life,* and this from its very origins in the lateral furrow of the medulla oblongata.

A Typical arrangement.—In the constitution of the metamere, such as that which corresponds to a spinal nerve pair, or even to the trigeminal, the separation of the sensory and motor functions on the one hand, conscious and unconscious on the other, affects a typical arrangement which much facilitates the analysis and the detailed description of these functions. In the pneumogastric nerve, this externally apparent systematization has almost disappeared, through the intermixture and intricacy of the different elements after leaving their place of origin.

Nucleus of origin.—The nucleus of origin of the tenth pair is a mixed nucleus, enclosing elements whose functional value differs greatly. It receives a large number of centripetal fibres, among which the elements of unconscious sensation predominate, along with fibres of conscious sensation. It is the point of origin of a certain number of terminal neurons which proceed to the voluntary muscles ; it gives off a much larger number of which the terminations are arranged in a graduated manner in the ganglionic masses belonging to the great sympathetic, thus showing in an obvious way the functional relations which this nerve maintains with the system of vegetative life.

Jugular and plexiform ganglia.—At its exit from the skull, the pneumogastric presents two ganglionic enlargements (*jugular ganglion* [*ganglion of the root*] and *plexus gangliformis* [*ganglion of the trunk*]), which their structure designates as the

equivalents of a spinal ganglion, at least as regards the larger portion of their elements, but without, nevertheless, it being possible to affirm that they do not partially correspond to a great sympathetic ganglion.

Field of distribution.—Taking origin in the medulla oblongata and soon anastomosing with important nerves, among which is the spinal accessory which yields to it its internal branch, the pneumogastric exhausts itself in ramifying successively in the neck, the thorax and the abdomen. Its inferior limits are not well determined because, falling into a complicated system made up of ganglionic relays which also contain fibres passing through them, we have no anatomical or experimental method which is well adapted to determine the localities in which its fibres terminate; these terminations being, further, arranged in a graduated series over a certain number of these relays. The pneumogastric is formed of fibres, some of which are myelinated, others non-myelinated. These

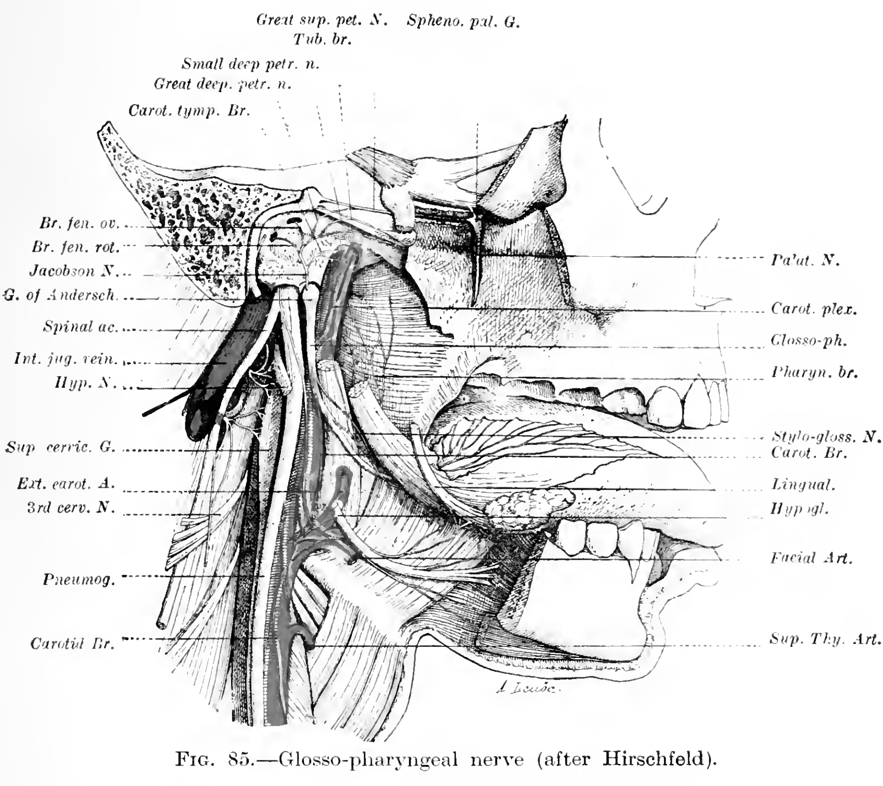


FIG. 85.—Glosso-pharyngeal nerve (after Hirschfeld).

latter are present in it in great number, and the former are in it much reduced in size. These characters approximate them to those of the great sympathetic.

Protoneurons and intercentral neurons.—The elements of conscious sensation and of voluntary movement which the pneumogastric contains are confined to the neck and proceed chiefly to the larynx. Hence they are obedient to the law of metamerism, which demands that their terminations should be contained in the same segment of the body as that which includes their origins, or nearly so. They are *initial or terminal neurons, or protoneurons.* On the other hand, the elements of unconscious and involuntary function break altogether with metamerism; in doing this they reproduce the arrangement of the great sympathetic

chain, which forms communications, no longer between the organs of a metamere, but between the different metameres themselves, for the functions as a whole. The greater portion of the fibres of the pneumogastric are thus equivalent to *intercentral fibres*, which connect an important region of the grey axis (medulla oblongata) with the nuclei directly motor in function, of organs which are essential to life (ganglion of the great sympathetic).

Specific functions.—If, in the pneumogastric, the line of division between sensation and motion, and even between the conscious and unconscious, is not obvious at first sight, there is another which concerns the specific nature of the functions, and which is on the contrary very evident. This large assemblage of nerves exhausts its ramifications in three great apparatus: that of *respiration*, that of *circulation*, and that of *digestion*, which it helps to individually govern, and also to mutually harmonize amongst themselves, in union with other portions of the great sympathetic system. Yet the elements of specific functions, apart from the fact that they are each of them of different modalities (centripetal, centrifugal, motor, inhibitory, secretory, etc.), before they attain their terminations, are mixed in the branches, which often contain them united

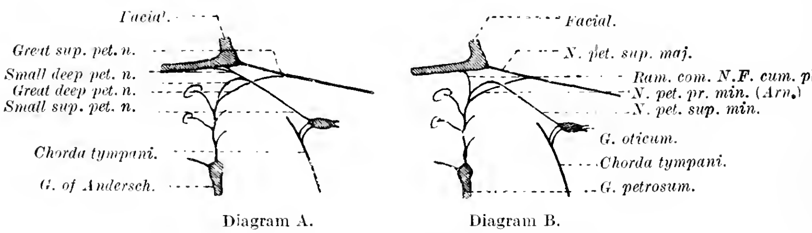


FIG. 86.—Diagram of the terminal branches of the branch of Jacobson.
A, French nomenclature; B, German nomenclature.

one with another. Thus we are forced to make an analytical and detailed review of them in connecting them only with their chief functions.

A. RESPIRATION.—Respiration is represented in the vagus by the nerves, some centripetal, others centrifugal, which preside over very diverse kinds of acts.

Superior laryngeal branch.—The upper portion of the larynx, the arytæno-epiglottidean folds, the epiglottis, the posterior and inferior portion of the tongue, derive from this nerve (chiefly by the *superior laryngeal* branch), the acute sensibility with which these regions are endowed, and which gives rise to the expulsive cough following the introduction of the least drop of liquid falling on the aperture of the glottis.

The trunk of the vagus, when the nerve is cut in the region of the neck, is but slightly sensitive; it contains nevertheless a large quantity of subconscious sensory elements which are distributed to the inferior portion of the larynx and the trachea (*inferior laryngeal or recurrent nerve*), the œsophagus, the pulmonary tissue, the stomach, and doubtless also the intestine and the liver.

By *the anastomosis of Galen*, which connects the superior laryngeal

nerve to the recurrent, the lower portion of the larynx and the trachea receive sensory elements from the first of these nerves (Philippeaux and Vulpian ; Fr. Franck), in addition to those which they receive from the second.

Sensitiveness of the different portions of the larynx.—The great difference which exists between the sensitiveness of the superior and the inferior portions of the larynx can be shown experimentally : water injected from above downwards (upon the opening of the glottis) gives rise to a loud expulsive cough ; when injected from below upwards (by an opening made in the trachea), this defensive reflex does not arise.

Dyspnœa.—No more than it suppresses hunger, does section of the two vagus nerves in the neck do away with the necessity of breathing. On the contrary, it may be said that it increases that necessity. Respiration becomes slower and deeper, assuming the characteristics of that which is known as dyspnoea.

Eeffcts of the stimulation on the respiratory movements.—*Stimulation of the superior end of the cut vagus hastens, on the contrary, the respiratory rhythm,* and this so much the more as the stimulation itself is the more intense ; it may arrest the movements of the diaphragm and of the thorax, either in inspiration or in expiration, according to the branches excited, or according to the gaseous composition of the blood. This arrest is due to a tetanic contraction of one of the two orders of muscles, combined with inhibition of those of the opposite order.

Reflex sensibility of the viscera.—Doubtless the vagus nerve represents the sensory element of a considerable number of reflex phenomena which are observed as regards the vegetative functions, and double section of the nerve should induce in the latter various perturbations ; but these are not rendered obvious by disorders which are immediately visible like the preceding.

Recurrent nerve.—With the exception of the cricothyroid, which is innervated by the superior pharyngeal nerve, all the muscles of the larynx are supplied by the recurrent or inferior laryngeal nerve.

Original and borrowed elements.—The pneumogastric in the region of the neck contains a large number of fibres which take part in very diverse motor functions ; these fibres come, some from the same origins as those of the tenth pair, and others from anastomoses with the neighbouring nerves, especially the spinal accessory, with regard to which we shall refer to them again. The movements of dilatation which the glottis performs at every inspiration must equally appertain to the pneumogastric, for they persist after the extirpation of the

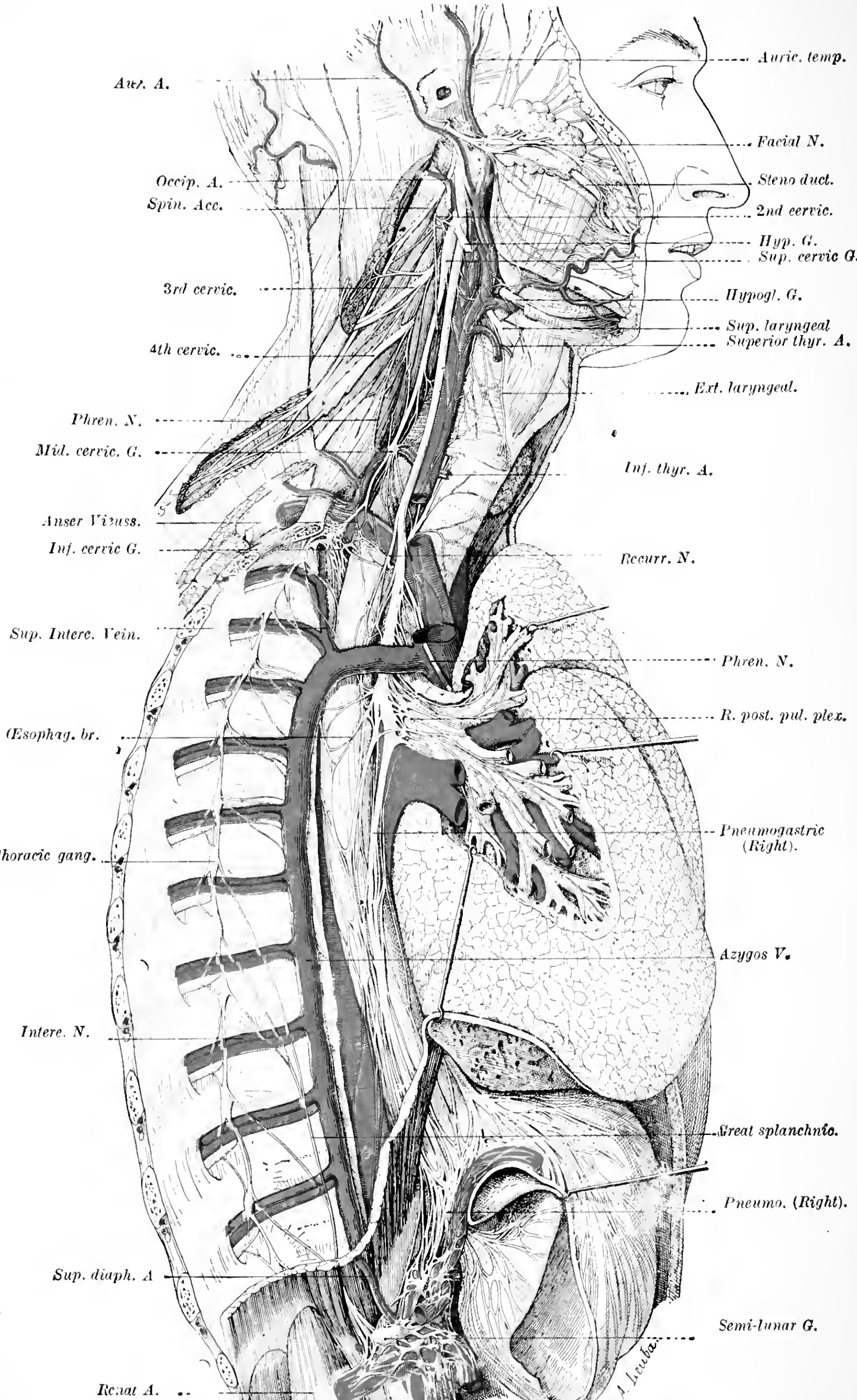


FIG. 87.—Pneumogastric.

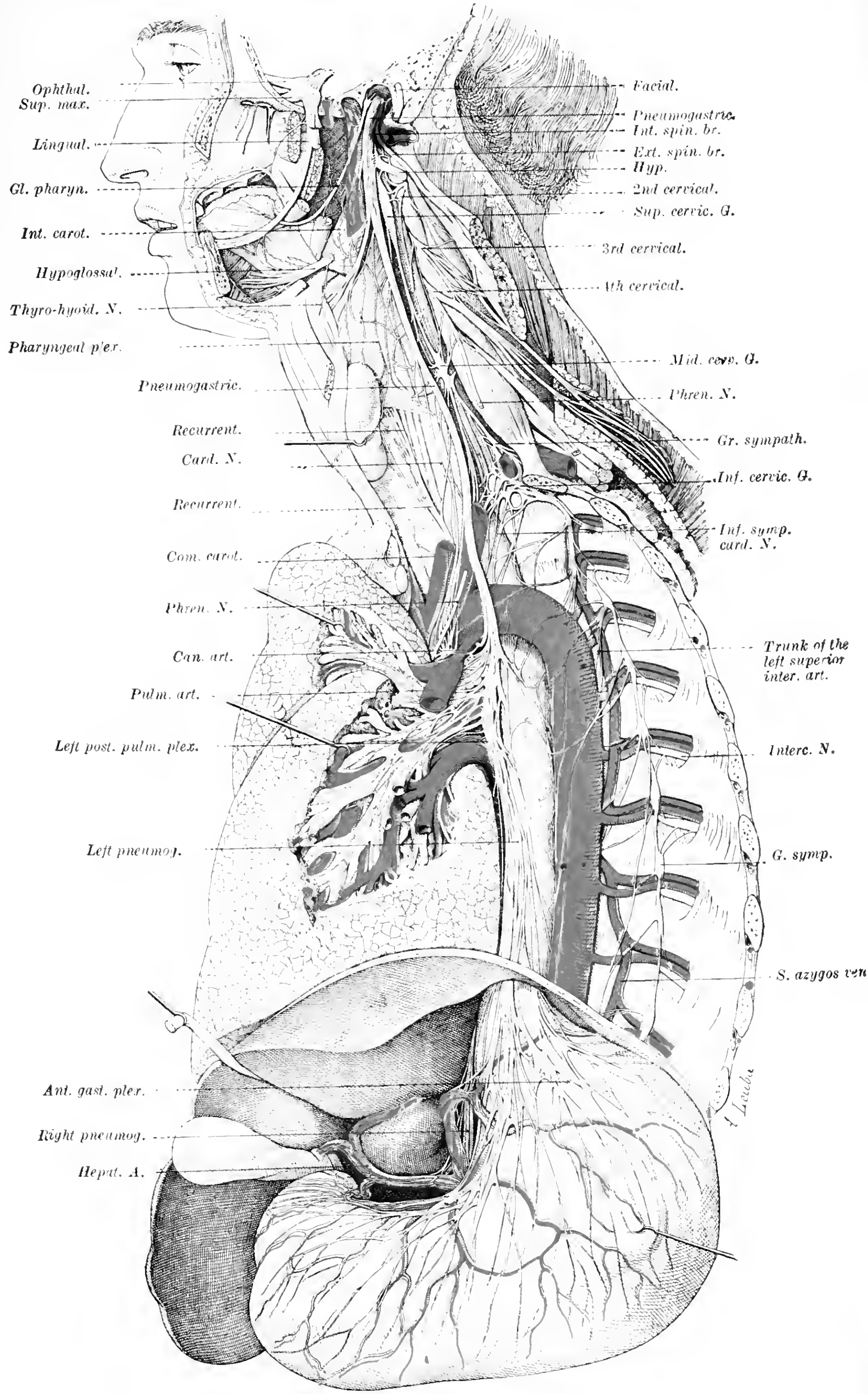


FIG. 88.—Left pneumogastric.

spinal accessory ; but the vocal movements of the larynx (narrowing of the glottis and tension of the vocal cords) are then suppressed (Cl. Bernard).

Pulmonary nerves ; motor, inhibitory.—The membrane of the trachea, the large and small bronchi, and even the pulmonary vesicles (according to some authors), contain smooth muscular elements (fibres of Reissessen), whose contractions are very slow. The pneumogastric supplies them with motor elements (Williams, P. Bert), and also with inhibitory elements (M. Doyen). The action of the one causes narrowing of the pulmonary passages regarded as a whole, that of the others permits of their distension under the influence of the very feeble pressure of the air which they contain. In order to make the inhibitory effect apparent, a device must be made use of to dissociate the two effects. The ordinary effect of stimulation of the vagus is that of narrowing (motor effect). In the case of an animal submitted to the action of pilocarpine, on the contrary, the inhibitory effect or that of dilatation is the one which results.

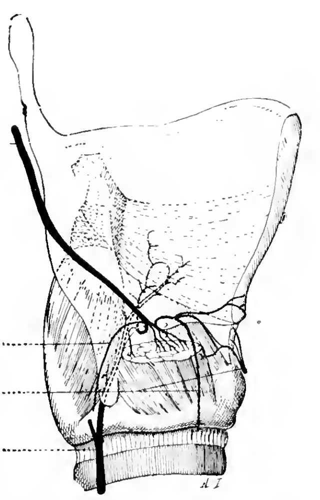


Fig. 89.—Distribution of the nerves in the human larynx (semi-diagrammatic) (after Exner).
Lateral aspect. The thyroid cartilage is supposed to be transparent.

Vaso-motor effects.—Section of the vagus nerves is followed by pulmonary congestion, so marked as to be of the nature of red hepatization. The laryngeal nerves, especially the superior, contain vaso-dilator and secretory fibres for the mucous membrane of the larynx (Hedon).

B. Circulation.—The vagus supplies both centripetal and centrifugal elements to the heart, whose modes of action are so characteristic that they are cited as typical examples of this species of functional activity.

Depressor Branch.—In the rabbit, the vagus possesses a branch of sensory nature which comes to it from the heart tissue, and which joins it in the angle of separation which the superior laryngeal branch forms with it. Stimulation of the peripheral end of the cardiac branch has no effect on the heart, but that of the central end reacts on the

general circulation *by lowering the aortic arterial pressure* through a double mechanism : the *stimulation* is indeed *reflected*, on the one hand on the elements which stop the heart, whence ensues slowing of the beats of the organ ; and on the other hand *on the vaso-dilators of the deep areas*, especially of the intestine, whence results diminution of the resistance which opposes the flow of the blood in the general capillaries, and in this way lowering of the general arterial pressure (Ludwig and Cyon). It is owing to this phenomenon that the nerve has received the name of *depressor*.

Thus stimulation of the depressor nerve is followed by complex effects ; indeed. it acts in an opposite manner on certain departments of the vascular system ; thus, while it causes dilatation of the intestinal vessels, it contracts the capillaries of the skin, which effect is especially visible when the auricular artery is observed (Dastre and Morat) ; but nevertheless, the chief effect is a general lowering of arterial pressure. The depressor nerve regulates arterial tension.

Cardio-inhibitory elements.—The stimulation of the pneumogastric in the neck (or that of its cardiac branches) *stops the contraction of the heart by causing diastole of the myocardium.* This is the first example of stoppage of action arising from the nervous system, or, as it is now termed, of inhibition, which has been observed (Weber, 1845).

According to the intensity of the excitation. the heart is either totally arrested or only slackened. Stimulation of *one* only of the two vagus nerves suffices to produce either slowing or stoppage. The inhibitory action of the right vagus is usually far more marked than that of the left (Arloing and Tripier).

Their origin.—The cardio-inhibitory elements contained in the pneumogastric do not arise from the origins of the latter, but from the internal branch of the spinal accessory, as do also a certain number of other centrifugal elements of the tenth pair. They originate, therefore, in the inferior portion of the medulla oblongata.

Cardio-accelerator elements.—When atropine is made use of in very small doses (less than a milligramme), paralysis of these cardio-inhibitory elements results, which are then no longer excitable. Stimulation of the trunk of the vagus (in which the action of these fibres has been eliminated by this means) then accelerates the heart beats, which proves that it contains a certain number of accelerator elements independently of those which are supplied to the heart by the great sympathetic (Fr. Franck).

Their Origin is Distinct from that of the Preceding.—If the trunk of

the vagus be stimulated, either acceleration or slowing of the heart may ensue, according to circumstances. If, on the other hand, the lower portion of the medulla oblongata be stimulated, after the latter has been separated from the spinal cord, only slowing or stoppage is ever seen (Heidenhain). Hence, the cardio-inhibitory elements arise from the medulla oblongata, while the cardio-accelerator elements (even those contained in the trunk of the vagus) take origin in the spinal cord.

C. Digestion.—Like the respiratory apparatus and the heart, the digestive tract in the whole of its upper portion derives a part of its innervation over a large area from the pneumogastric. Like these same apparatus, the nerve supply is not drawn entirely from this nerve, but it completes this supply by drawing upon a portion of the great sympathetic. It is worthy of notice that the nature of the action exerted by each of these nerves on each of these apparatus is different, indeed opposed, inasmuch as the one is, for example, inhibitory, while the other is motor for a given organ. Further, it is to be noticed that the nature of the action of each nerve is not univocal, each of the two nerves being motor for one organ, while it is inhibitory for the other. Also the functional opposition which exists between the two nerves is not absolute : each of the two is a mixture of antagonistic fibres, but in unequal proportions.

Pharyngeal branch.—The pharynx, a sensory surface, is innervated by the pharyngeal branch concurrently with the branches of the ninth pair. This is also the motor branch for the three constrictor muscles of the pharynx.

Deglutition.—As in the stomach and in the pharynx, the œsophagus receives from the pneumogastric both sensory and motor elements, which take part in the performance of the complicated act of swallowing. Although reduced in the œsophagus to a mere movement of peristaltic propagation, the muscular nervous mechanism which is its foundation is far from being understood, in spite of the experimental analysis to which it has been submitted by many observers.

In the dog there is a special arrangement : the superior portion of the œsophagus receives its nerves from a branch given off from the superior cervical ganglion of the sympathetic (Espézel).

Muscular sensibility of the œsophagus.—The pneumogastric gives sensory nerves to the œsophagus ; it distributes them not only to the mucous membrane, but also to the œsophageal muscles, whose movements they co-ordinate, by one of those reflex and automatic acts of which so many are now known.

Part taken by sensation in the movements of the œsophagus.—The

movements of the œsophagus are almost as severely disturbed by section of its sensory fibres as by that of its motor nerves. Independent section of each is possible in certain animals for a given area of the tube. at all events to a certain extent. In some, indeed, such as the horse, the ass, the dog, the sheep, the motor fibres which are destined for the cervical portion of the œsophagus leave the vagus with its pharyngeal and external largyngeal branches; while the sensory fibres proceed from the branches given off lower down. In other animals, such as the rabbit and possibly man, the motor elements attain the œsophagus by the roundabout route of the recurrent (Chauveau). Stimulation of the sensory fibres, like that of the motor fibres, causes contraction of the œsophagus, but does not give rise to the peristaltic action which is its normal movement; it produces merely a more or less complete *tetanic* contraction of its muscles (Chauveau).

Gastric sensibility.—Seeing that the pneumogastric proceeds to the stomach, it has been asked if it is not the "nerve of hunger," considered thus as a special sensation whose external field would be the digestive tube (wholly or partially), and the vagus nerve the aggregation of its conducting elements. This is not the case; after section of both vagus nerves, an animal still experiences the sensation of hunger.

General needs.—Hunger, like thirst or the need of breathing. is in reality a specialized sensation in the sense that we can define it amongst other sensations; but the field of excitations which give rise to it is (like that of other analogous sensations) more or less generalized to all tissues and all the cells of the organism. Nutrition, to which it corresponds, is not indeed confined to the digestive organs, but is a general fact like life itself.

Specific nature and unconsciousness.—From another point of view, the sensibility of the gastric mucous membrane seems to be special and connected with certain acts which it controls and provokes; but this sensibility is unconscious or sub-conscious: thus *the pylorus only opens for the passage of aliments into the intestine when gastric digestion is ended*, and this implies a sensory phenomenon which might by comparison be called gustatory.

Stimulation of the origins of the vagus.—Stimulation of the roots of the vagus nerve causes contraction of the muscles of the pharynx and of the œsophagus, and at the same time induces movements in the stomach (Chauveau).

Stimulation of the Trunk.—Excitation of the vagus in the neck gives every facility for observing, not only the movements of the stomach,

which are the consequence of it, but also for studying their character. These movements are rhythmical, as is shown by the tracings which can be obtained of them by placing an ampulla in the gastric cavity, and they are doubtless transmitted in a peristaltic manner through the length of the organ from one of its orifices to the other. The line of tracing does not touch zero so long as the stimulation lasts, which indicates a continuous pressure exerted by the stomach on its contents.

Thus the vagus nerve is the excito-motor nerve of the stomach, but it also contains some inhibitory elements which can be demonstrated in a reflex manner, by exciting, for example, the central end of the opposed vagus (Morat), or by stimulating a nerve of general sensation (Wertheimer).

In certain animals, stimulation of the vagus gives rise to rhythmical contractions of the upper portion of the intestine. The motor effects are mingled with, or followed by, inhibitory results. A vaso-motor influence on the stomach and the upper portion of the intestine is also recognized as belonging to the pneumogastric (Pingus).

Secretory elements.—Not easily demonstrated as regards the stomach, the secretory effects of stimulation of the vagus are very definite in the case of the *pancreas* (Afanasiew and Pawlow, Morat). So far as concerns the *liver* (secretion of bile, formation of sugar), the action of the tenth pair is not easy to determine. Stimulation of the central end of the vagus usually causes dilatation of the sphincter, which is situated at the extremity of the bile duct, while it induces contraction of the gall bladder (Doyen). Stimulation of the central end acts also on the liver by augmenting the glycogenic secretion (Cl. Bernard, Filhene, Laffont).

Stimulation of the peripheral end usually diminishes the circulation in the kidney and the secretion of urine (Arthaud and Butte); it acts equally on the bladder, by making it contract (Œhl). By irritating the central end, Germain See and Gley have induced azoturia.

D. **Trophic action.**—Section of the vagus nerve is followed by very various alterations affecting the organs which are supplied by this nerve, alterations which affect the muscles, the mucous membranes and the parenchyma of these organs. Atrophy of the muscles of the larynx has been observed, degenerations (but limited to some fibres) of the myocardium, hæmorrhagic and interstitial lesions of the gastric mucous membrane. In the lung, especially, emphysema, nuclei of congestion and of red hepatization have been noticed; in the kidney, fatty and hyaline degeneration. Alongside these disorders of an anatomical nature, others have been met with which the chemical study of the organs and of the media have brought into notice: namely, a diminution in the gaseous exchanges through the lung, a diminution of the hepatic glycogen, which is at

first accompanied with a hyperglycæmia, afterwards with a hypoglycæmia. These disturbances of the animal chemistry, which it is the custom to describe as "trophic," are, fundamentally, functional disturbances of organs specially set apart for the purpose of general nutrition of the organism. This suffices to show that the expression *trophic* does not properly characterize them. Specifically, they are of very complicated mechanism, the lesion of one organ reacting on the functional activity of other remote organs and thus inducing new alterations.

Its complex mechanism.—When the vagus nerves have been cut, and in this way the impulses which these nerves supply to certain organs have been abolished, the initial lesion of these organs belongs to the order of degenerations which follow the lack of functional activity (atrophic degeneration of the muscles, analogous alteration of the glands of the parenchyma and of the epithelium). These disturbances are increased by the circulatory disorders which result from the section of the vaso-motor nerves contained in the pneumogastric. The functional inertia which is at the foundation of these degenerations may result from the depression of nervous influences, some directly motor (the ordinary case), the others indirectly motor by reflex action (the case of atrophy of the larynx which ensues, as Exner has observed, after section of the superior laryngeal nerve, a nerve pre-eminently sensory).

The lesion once established, when it is located in such an organ as the lung disturbs an essential function : hematosis. A certain degree of asphyxia results whose usual consequences then manifest themselves. They are especially shown by the premature consumption of the hepatic glycogen, by hyperglycæmia, and finally by hypoglycæmia, with its very serious consequences (Couvreur).

Reaction at a distance.—Important organs like the liver, the pancreas, without speaking of the kidney and the digestive tract, are in a way attacked, and directly so, by the suppression of the relations, both centripetal and centrifugal, which they maintain with the superior centres, and indirectly, by the alterations of the composition of the blood, on which they themselves regulate their own functional activity. Section of the two vagus nerves, on account of the great number of organs to which these nerves are distributed, thus induces an extreme disturbance of the conditions on which the nutritive equilibrium of the organism depends. It is through the definite loss of this equilibrium, much more than through any localized phenomenon or accident, that death ensues after double vagotomy.

Double vagotomy.—Section of a single pneumogastric nerve does not involve death. The two nerves, indeed, easily supplement one another, doubtless owing to the reciprocal interpenetration of their areas of distribution. Double section involves death in the dog after about three or four days, but sometimes the delay is longer. It varies according to the animal : survival is especially long in birds and reptiles. If, between the two sections, a period sufficient for nerve regeneration is allowed to elapse, the animal survives (Philippeaux).

g. Spinal Accessory.

The spinal nerve, the *accessory* nerve of Willis or of the eleventh pair, has an arrangement and performs functions which are somewhat special. This nerve has its origins in the medulla oblongata, and these are prolonged from those of the pneumogastric (in the collateral furrow), and it has also origins in the spinal cord, which are independent of those of the cervical nerves. From this point of view,

indeed, it is rather a supplementary spinal nerve than an accessory one, because it discharges an important function. This nerve is not found in fishes and the amphibia. It first shows itself in reptiles as a branch of the vagus.

Boundaries.—Willis regarded these spinal cord origins, and the so-called external branch which continues them, as being the whole of the spinal accessory nerve ; the bulbar roots and the internal branch which originate from it were, on the contrary, grouped by him with the trunk of the pneumogastric. Scarpa reunited the two branches (medullary and bulbar) in one and the same description, because, united to each other in the posterior lacerated space, they there form a single nerve trunk ; and this is a description which has since been given of them.

Essentially motor function.—The branches of origin of the nerve

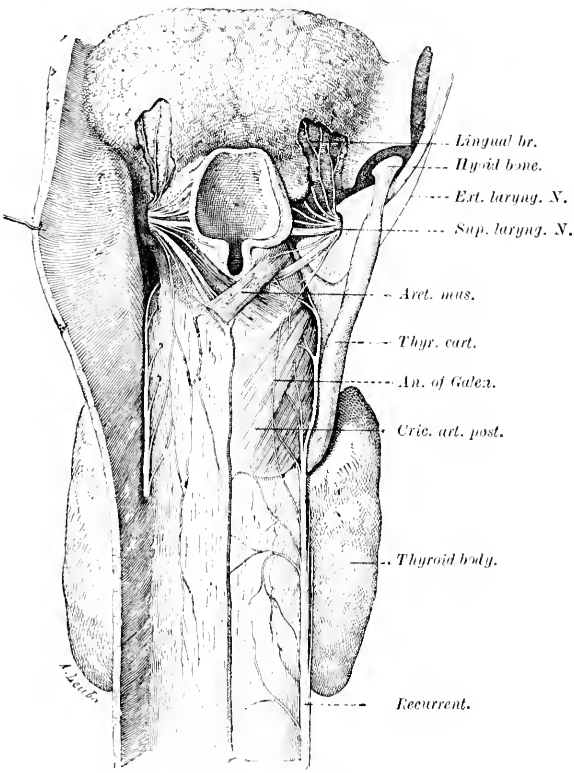


FIG. 90.—Terminal branches of the recurrent.

sometimes bear, one or the other exceptionally, on their course, a ganglion of which it is difficult to say whether it is sensory or sympathetic. Experimentally, sensory elements have not been ascertained to exist in this nerve, which is assumed to be exclusively motor.

Isolated destruction by tearing out of the nerve.—Cl. Bernard has devised a method which allows, in young animals, the isolated destruction of the root of the spinal accessory, by means of a trivial operation not attended with great destruction, and which assures the survival of the subject. It consists in the tearing out of the nerve, which has been previously laid bare at its exit from the posterior lacerated space.

Carefully adapted progressive traction on the nerve breaks down the adhesions by which its conjunctival sheet is attached to the bony canal, and the forceps which are then applied to it brings away a long portion which represents its roots both medullary and bulbar.

It is possible, indeed, but with some risk to the success of the experiment, to tear out separately either the medullary roots or the bulbar roots by grasping separately either the external or internal branch (Cl. Bernard).

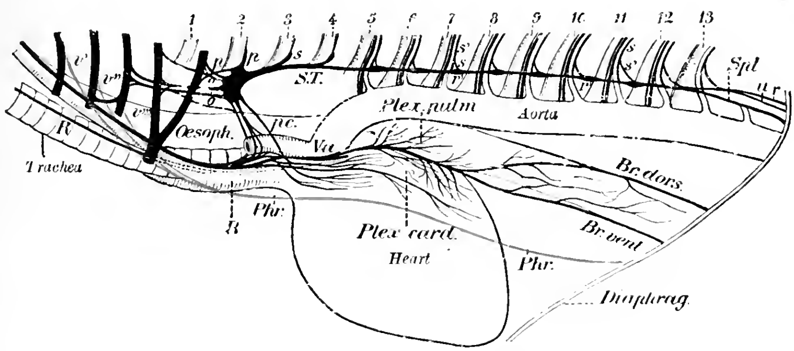


FIG. 91.—The principal nerves of the thorax in the dog (copied from Ellenberger and Baum).

Phr, phrenic (in red) with its three roots, v', v'', v''', arising from the 5th, 6th and 7th cervical.
Va, pneumogastric with its cardiac, œsophageal and pulmonary branches and the recurrent nerve R.
ST, sympathetic thoracic chain with its ganglia r, r'; s, s', intercostal nerves and their communicating branches proceeding to the sympathetic chain; p, first thoracic ganglion and its branches of union with the first thoracic nerves; o, its branches of union with the last cervical pairs (vertebral nerve); *pc*, its cardiac branch and to the left of this the Ansa Vieussenii by which the thoracic sympathetic becomes continuous with the cervical sympathetic united to the trunk of the pneumogastric; *Spl*, great splanchnic; u, small splanchnic; 1 to 13, divided ribs accompanied by the vessels and intercostal nerves.

A. INTERNAL BRANCH.—**Vocal function of the spinal accessory.**—Destruction of the spinal accessory, or merely of its internal branch, if effected on one side only, produces *hoarseness of voice*, and if made *on both sides*, completely *suppresses* the *emission of sounds* (Cl. Bernard).

Hoarseness, Aphonia.—Hoarseness or aphonia is the consequence of the paralysis of the chief constrictor muscles of the glottis.

If, indeed, in an animal in which the spinal accessory is destroyed, the thyro-hyoid membrane be split so that the movements of the larynx may be directly observed, it is seen that its superior orifice continues dilated, there being no power to completely close it. There are, indeed, slight alternate movements of dilatation and closure ; but

these movements are those which are always observed in the larynx, inasmuch as they accompany every movement of inspiration and expiration of air, in the same manner as the movements of dilatation and contraction of the nostrils.

Respiratory function of the vagus.—If, after having (by destruction of the spinal accessory) rendered impossible the movements of the vocal cords, the trunk of the vagus or, rather, the recurrent nerves, be cut, the respiratory movements of this organ, the larynx, will also disappear. The orifice of the larynx not only no longer dilates, but is narrowed and immobilized, and if the experiment is made on a young animal (in which the softer membranes yield under the current of inspired air), asphyxia may ensue.

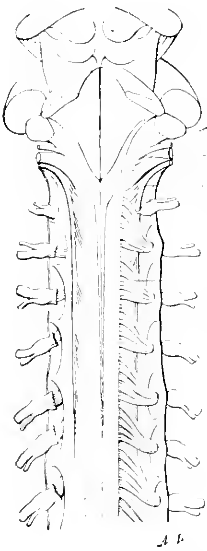


FIG. 92.—Apparent origins of the glosso-pharyngeal, pneumogastric, and spinal nerves.

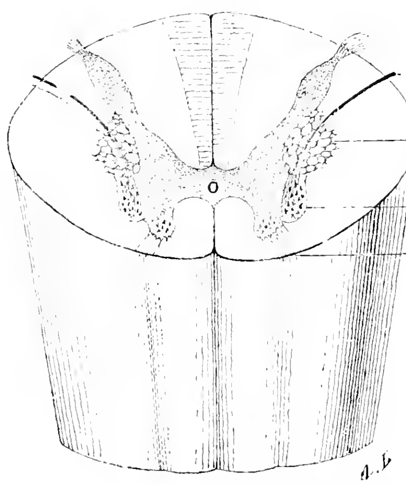


FIG. 93.—Real origins of the medullary portion of the accessory.

Antagonistic nerves and muscles.—Thus the larynx performs two orders of movements, which correspond to two distinct functions in a certain degree antagonistic; the *vocal* function and the *respiratory* function. Certain muscles, like the posterior crico-arytænoids, whose dilating action is evident, have a more exclusively respiratory function; certain others, like the lateral crico-arytænoids, the thyro-arytænoids, the arytænoids, the crico-thyroids, which approximate and make tense the inferior vocal cords, possess a more exclusively vocal function.

However, the vocal and respiratory functions make use now of the one, now of the other of these muscles for the execution of movements which only differ in their result. It is therefore rather the nervous elements which preside over them which are functionally distinct and in a certain measure antagonistic. Analdson, Fr. Hooper, Livon have endeavoured to dissociate, by physiological

methods, these elements scattered in the trunk of the recurrent nerves. According to Livon, it is possible, by varying the *rhythm* of the stimulation brought to bear on these latter nerves, to obtain distinct effects of occlusion or of dilatation of the glottis. Dilatation is, however, accompanied with movements which are synchronous with the excitation (animals under the influence of chloroform, chloral and morphia, and an ampulla in the glottis for the record of movements).

Recurrent Nerves.—The nerve fibres which come, some from the origins of the spinal accessory (for the vocal cords), the others from those of the vagus (respiratory fibres), after mixing momentarily in the trunk of the vagus, proceed to the larynx, chiefly by means of the recurrents, with the exception of those which go to the crico-thyroid, conveyed thither by the superior laryngeal. Hence, if either the trunk of the vagus or that of the recurrent be cut, both sets of fibres are divided at the same time: phonation becomes impossible and the respiration is embarrassed.

Asphyxia.—In very young animals, section of the recurrent nerves (and consequently of the vagus) may be followed by immediate asphyxia; while in older animals, respiration remains possible, although it may be slightly embarrassed (Legallois). This is owing to the fact that in the first the delicacy of the membranes of the larynx (boundaries of the glottis) causes them to act as valves when the glottis is opened at each inspiration, and in this way they produce an obstruction to the entrance of air, whereas in the second the greater rigidity of these structures causes an open space to be maintained through which the air can pass; this space is specially defined between the arytænoid cartilages (intercartilaginous portion) rather than between the vocal cords (interligamentous portion of the glottis) (Longet).

Superior laryngeal nerve, its motor function.—Section of the superior laryngeal nerve produces merely hoarseness of the voice, through paralysis of the crico-thyroid and want of tension of the vocal cords.

Stimulation of the origins; motor effects.—When the origins of the spinal accessory in the medulla oblongata are irritated, contraction of the superior constrictor muscle of the pharynx ensues (Chauveau). These motor elements are supplied to the pharyngeal plexus by the internal branch of the spinal accessory after it has entered the jugular ganglion of the vagus, conjointly with other branches coming from the vagus itself and the glosso-pharyngeal.

Cardio-inhibitory effects.—The internal branch of the spinal accessory originally contained inhibitory fibres which are destined for the cardiac muscle. If, indeed, this portion of the spinal accessory is cut or torn out, and if after an interval of some days (so that the cut fibres may have time to degenerate), the vagus be stimulated, this excitation no longer induces slowing or stoppage of the heart (Waller). This fact has been disputed by several observers; there may be individual variations in the origin of these nerves, and these varieties may be present in the two nuclei.

B. External Branch.—**Its function in exertion.**—The medullary portion of the origins of the spinal accessory forms outside the skull, the external branch of this nerve which supplies the sterno-mastoid and trapezius muscles. It forms, for these muscles, a nerve supply

superadded to that which they receive from the neighbouring cervical pairs, and which also appears to be connected with phonation, or rather with all effort which necessitates the suspension of respiration. Section of the spinal accessory, in so far as it supplies the trapezius and sterno-mastoid muscles, would immobilize the thorax, or more or less *suspend expiration*, in order to permit it to adapt the column of expired air to the modulations of the voice.

Section of the external branch permits the persistence of the voice, but the cries are shorter, and the animal soon *becomes out of breath.* From this point of view, the spinal accessory may be described as *the nerve of effort* (Cl. Bernard).

h. Hypoglossal Nerve

The hypoglossal, or nerve of the twelfth pair, is the motor nerve

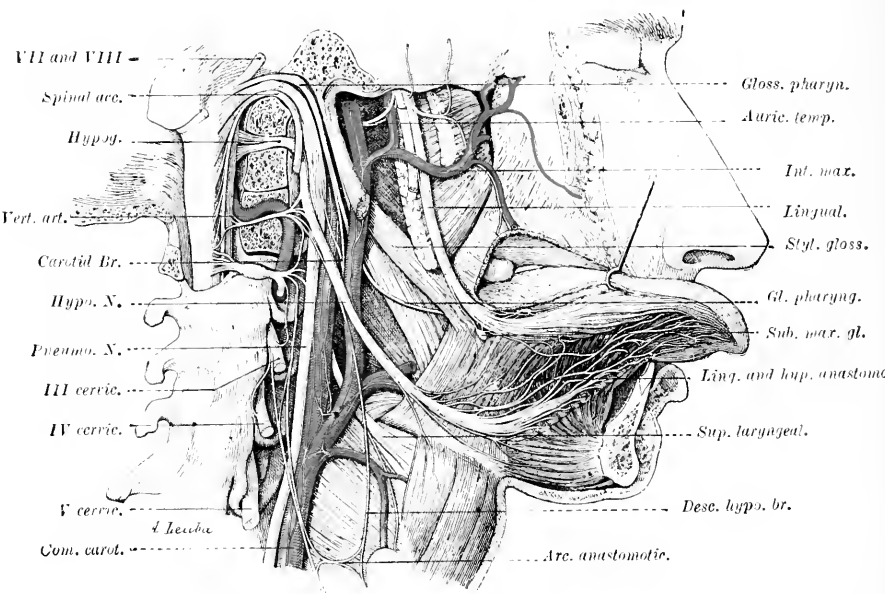


FIG. 94.—The hypoglossal nerve (after Hirschfeld).

of the intrinsic muscles of the tongue and of certain muscles of the neck. Being such, it assists in the movements of *mastication* and of *deglutition*.

1. **Effects of section ; motor paralysis.**—Section of the two hypoglossal nerves in the dog considerably embarrasses these two orders of movement. Nevertheless, according to Philippeaux and Vulpian, it does not render them absolutely impossible, as Panizza affirms. After some time, the animal, by divers movements, compensates the

inactivity of the tongue. This latter, although having lost its intrinsic movements, is not on that account rendered completely immobile, but movements are communicated to it by the muscles of the region of the neck, which are partially innervated as much by the trigeminal as by the facial or the cervical nerves.

The hypoglossal is obviously distributed, not merely to the intrinsic muscles of the tongue, but to a considerable number of those of the anterior portion of the neck. But as regards several of the latter, this is a borrowed motricity, inasmuch as the nerve of the twelfth pair forms two important anastomoses with the cervical plexus.

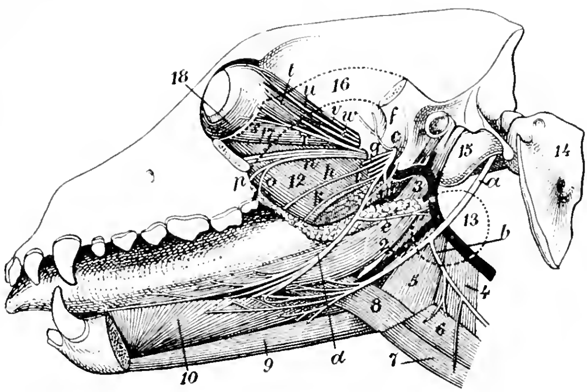


FIG. 95.—Principal nerves of the head in the dog (after Ellenberger and Baum).

a, hypoglossal nerve ; *b*, its descending branch ; *c*, inferior maxillary branch of the trigeminal ; *d*, lingual nerve ; *e*, chorda tympani ; *f*, deep temporal nerve ; *g*, pterygoid nerve ; *h*, buccinator nerve ; *i*, inferior dental nerve ; *k*, branch going to the soft palate ; *l*, chorda tympani before its entrance into the lingual nerve ; *m*, mylo-hyoid nerve ; *n*, spheno-palatine nerve ; *o*, posterior palatine nerve ; *p*, anterior palatine nerve ; *q*, sub-orbital nerve ; *r*, orbital branch of the superior maxillary nerve ; *s*, branch of the oculo-motor proceeding to the inferior oblique muscle ; *t*, lachrymal nerve ; *u*, frontal nerve ; *v*, pathetic nerve ; *w*, external-oculo-motor nerve.

1, common carotid artery (in black) ; 2, lingual artery ; 3, internal maxillary artery ; 4, inferior pharyngeal muscle ; 5, middle pharyngeal ; 6, thyro-hyoid ; 7, sterno-hyoid ; 8, hypoglossal ; 9, genio-hyoid ; 10, genio-glossal ; 11, stylo-glossal ; 12, internal pterygoid ; 13, locality occupied by the sub-maxillary gland which has been removed : 14, atlas ; 15, tympanic bulla ; 16, zygomatic arch ; 17, inferior rectus muscle of the eye : 18, inferior oblique.

Superior anastomoses.—The first occurs at the level of the first cervical arch, and the other, much lower down, is effected by the descending branch.

Descending branch.—The descending branch of the hypoglossal descends to meet the branch of the same name given off by the cervical plexus, by forming a loop, from which are detached branches for the sub-hyoidean muscles (omo-hyoid, sterno-hyoid, sterno-thyroid). Some observers, with Holl, Beevor, and Horsley, maintain that the hypoglossal is distributed only to the intrinsic muscles of the tongue, and that the branches which are given off from it before its termination

are furnished by these two anastomoses, following two direct or more or less recurrent tracts. Wertheimer has observed (in the dog) that, after section and degeneration of the descending branch of the cervical plexus, stimulation of the hypoglossal causes contraction of the sterno-hyoid and thyro-hyoid muscles of the sub-hyoid region.

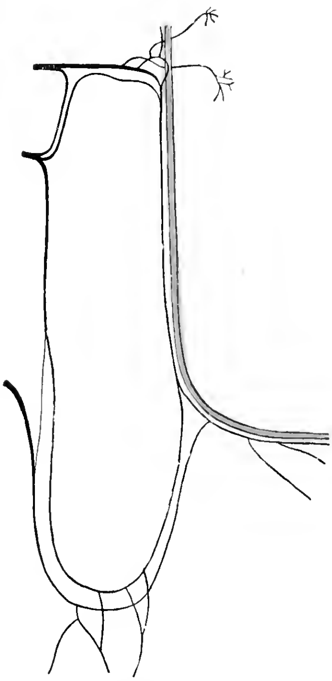


Fig. 96.—Diagram showing the relations of the hypoglossal nerve and the first cervical nerves (after M. Holl).

The cervical roots in black; the hypoglossal nerve in yellow.

2. **Sensation by anastomosis.**—The origins of the hypoglossal are exclusively motor (save for a small ganglionic root, which is in no respect constant, and which, when it occurs, must be regarded as the equivalent of a posterior root). After its exit from the anterior condyloid foramen, this nerve becomes sensory through the anastomoses which come to it either from the cervical plexus at its exit, or from the lingual, near to its termination. This borrowed sensibility is furnished to it by anastomoses, some direct, others recurrent, especially by the anastomotic loop which it forms with the lingual.

3. **Ganglionic Anastomosis ; Vaso-constrictor Elements.** — From the superior cervical ganglion the hypoglossal receives an anastomosis by which the great sympathetic supplies the vessels of the tongue with a large proportion of their constrictor elements ; the others come to it by the lingual, together with the dilators.

If, indeed, in an animal curarized to the utmost available extent (in order to avoid intrinsic contractions of the tongue) the peripheral end of the cut hypoglossal be stimulated, the tongue will be observed to become pale through constriction of its vessels.

BIBLIOGRAPHY.

Metamerism; Embryological Data.—E. PERRIER, Les colonies animales —PRENANT, *Internation. Monatschr. f. An. und Phys.*, 1894, X, 6.—REMAK, Untersuchung üb. die Entwikel. der Wirbelth., Berlin, 1850, 1855.

Metamerism; Disturbances of Sensibility and of Nutrition.—BRISSAUD, *Presse méd.*, 1891, p. 17; *Sem. méd.* 1898, p. 385; Leçons sur les maladies du système nerveux.—DROUIN, Thèse Paris, 1898.—FIRMIN, Thèse Paris, 1850.—HEAD, *Brain*, 1893, p. 94.—HOUSSAY, *Arch. zool. exp. et gén.*, 1890, p. 187.—J. MACKENSIE, *Journ. of Path. and Bacter.*, 1893.—MARINESCO, *Neurol. Centralbl.*, 1892; *Arch. Phys.*, 1894; *Sem. méd.*, 1896.—ROSS, *Brain*, 1888.—THORNBURN, A contribut. to the surgery of the spin. cord, 1889; Sensor. distrib. of spin. nerves, *Brain*, 1893.—SHERRINGTON, *Philosoph. Transact.*, 1893; *Journ. of Anatomy*, 1896.—STARR, *Brain*, 1894.

Functions of the Nerve Roots.—Former Opinions.—BOERRHAAVE, De morbis nervorum, in-12, 1761, t. II, p. 695 et 696.—DULAURENS, Historia anat. hum. corp. et sing. ejus part. Trad. en français par Théophile Gelée, Paris, 1639.—GALIEN, De anatom. administr. lib. VIII, cap. v, p. 676 et suiv., édit. de Kühn, Leipzig, 1821; cap. ix, p. 696 et 697; cap. VI et VIII:—De methodo medendi;—De locis affectis, lib. I, cap. VI; lib. III, cap. XIV; lib. IV, cap. V et VII, d'après Longet.—LAMARCK, Philosophie zoologique, t. II, 1809, p. 260 et suiv.—RUFUS (d'Ephèse), De partibus corporis humani, trad. latine, édit. de Goupyl, Paris, 1554.—ALEX. WALKER, *Arch. of Universal Science*, juillet, 1809, t. III, p. 172.

Roots of the Nerves.—Experimental Period.—CH. BELL, An idea of a New Anatomy of the Brain, London, 1811 (travail à peu près introuvable, inexactement reproduit dans les éditions et publications ultérieures de CH. BELL et de SCHAW); exposition du syst. naturel des nerfs, trad. franç., Genest, Paris, 1825.—An exposition of the natur. syst. of nerves of the hum. body, with a republication to the papers delivered to the Roy. Society . . ., London, 1824; The nervous system of the hum. body, London, 1830.—E. FAIVRE, Étud. sur histol. comp. syst. nerv. Invertébr., Paris, 1857; *C. R. Ac. sc.*, 1857.—LONGET, *Arch. gén. de méd.*, 1841; Traité de physiologie, 3 edition, t. III, p. 102 et suiv.—MATTEUCCI et LONGET, *Ann. ch. et phys.*, 1844; *Ann. méd. psychol.*, 1844.—MAGENDIE, *Journ. phys. expér.*, t. I, 1821; t. II, 1822; t. III, 1823; Leçons sur les fonct. et les mal. du syst. nerv., 1839, t. II.—A. MOREAU (oiseaux, poissons), *Biol.*, 1858, 1859, 1860; *Ann. sc. nat.*, série 4, t. XIII, 1860.—JEAN MULLER (expér. sur les grenouilles). *Ann. sc. nat.* 1831, t. XXII, p. 95; Physiol. du syst. nerv., trad. Jourdan, t. I, p. 85; Manuel de physiol., trad. Jourdan, 1845, t. I, p. 559.—PANIZZA (chevreaux, grenouilles), Ricerche sperim. sopra i nervi, Pavie, 1834.—SCHIFF, Lehrb. d. Physiol. d. Mensch., p. 143.—VOLKMANN, *Arch. f. An. und Phys. Wissensch. Med.*, 1838, p. 15; 1841, p. 354.—VULPIAN, Leçons sur la physiol. gén. et comp. du syst. nerv., 1866.—WAGNER, Handwörterb. d. Phys. 1846.—YERSIN, *Bibl. univers. de Genève*, 1857.

Spinal Ganglia.—BARBIER, *C. R. Ac. sc.*, 1900, t. CXXX, p. 1039.—BETHE, *Arch. f. microsc. Anat.*, Bonn, 1897–98.—H. DALE, . . . Numeric. compar. of centrip. und centrifug. medull. nerv. fibres . . . spin. gangl., *Journ. of Phys.*, 1899–1900, p. 196.—EXNER, *Arch. f. Phys.*, Leipzig, 1878; *Sitz. d. K. Acad. d. Wiss.*, Wien, 1877.—GAD, Anat. et physiol . . ., *Arch. f. An. und Phys.*, 1887, p. 570.—GAD et JOSEPH, *Ibid.*, 1889, p. 199.—HUBER, *Journ. Comp. Neurol.*, 1897.—MAX JOSEPH, *Arch. f. An. und Phys.*, 1887, p. 296.—LANGLEY et ANDERSON, Action de la nicotine, *Journ. of Phys.*, 1892.—MORAT, Pouvoir transformateur des cell. nerveuses, *Arch. Phys.*—MOORE et REYNOLDS, *Journ. of Phys.*, 1898.—STEINACH, *Arch. f. d. ges. Phys.* LXXVIII.—WUNDT, Mekan. d. Nerv. 1876, Abth. 2, S. 567.

Centrifugal Elements of the Posterior Roots.—BAYLISS, *Journ. of Phys.*, 1900.—BONNE, Thèse Lyon, 1897.—CAJAL, *Anat. Anz.*, Iena, 1890, p. 112.—COSSY, *Arch. Phys.*, 1876.—GARTENER, *Wiener klin. Wochensch.*, 1889.—VAN GEHUCHTEN, *Anat. Anz.*, 1893, p. 215.—HERING, *Arch. f. d. ges. Phys.*. LXVIII, p. 6.—J.-F. HEYMANS et OV. d. STRICHT, Sur le syst. nerv. de l'Amphioxus et sur la constitution des racines sensibles, Bruxelles, 1898.—HORTON-SMITH, *Journ. of Phys.*, vol. XXI, p. 101.—JOSEPH, *Arch. f. Phys.*, Leipzig, 1887, p. 296.—KUHLWETTER, *Beitrag. z. An. und Phys.* (Eckhard), Giessen, 1885.—LENHOSSEK, *Anat. Anz.*, 1890.—MARTIN, *La cellule*, Louvain, 1895.—MORAT. *Arch. Phys.*, 1892, p. 689.—MORAT et BONNE, *C. R. Ac. sc.*, 1897.—RETZIUS, *Biol. Unter.*, Stockholm, 1892.—SHERRINGTON, *Journ. of Phys.*, 1894, p. 21; 1897, p. 209.—STEINACH, *Lotos*, 1893, t. XIV; *Arch. f. d. ges. Phys.*, LXXI, p. 554.—STEINACH et WIENER, *Arch. f. d. ges. Phys.*, t. LX, p. 593.—STRICKER, *Sitz. d. K. Acad. d. Wiss.*, Wien, 1876, t. LXXIV, Abth. 3; *Med. Jahrb.*, Wien, 1878.—VEIAS, Beitrag. z. Anat. und Phys. d. spin. gangl., Munich, 1883.—VULPIAN, *Arch. Phys.* 1878.—WANA, *Arch. f. d. ges. Phys.*, LXXI, p. 555.—VERZILOFF, *Centralbl. f. Phys.*, 1896.

Posterior Roots, Sensory Nerves, Trophic Disturbances.—Baerensprung, 1861.—Brissaud, Leçons sur les maladies du syst. nerveux.—Dejerine, *C. R. Ac. sc.*, 1876, t. LXXXIII, p. 281.—Morat, *C. R. Ac. sc.*, 1897, t. CXXIV, p. 1173.

Recurrent Sensibility.—Cl. Bernard, *C. R. Ac. sc.*, t. XXV, p. 104 ; Leçons sur la physiol. et la pathol. du syst. nerv., 1858, t. I, pp. 25–112.—Brown-Séquard, *Biol.*, 1850, t. II, p. 171.—Arloing et Tripier, Des conditions de la persistance de la sensibilité dans le bout périphérique des nerfs sectionnés, *Arch. de Phys.*, 1876, série 2, t. III. —Longet, *Gaz. des hôp.*, 1839 ; *Arch. gén. de méd.*, 1841.—Magendie, *C. R. Ac. sc.*, 1839.—Philippeaux et Vulpian, *Biol.*, 1859.—Vulpian, Leçons sur la physiol. gén. et comp. du syst. nerv., 1866.

Influence of the Posterior on the Anterior Roots.—Belmondo et Oddi, *Arch. ital. biol.*, 1891, t. XV, p. 17.—Dastre et Marcacci.—Cyon, *Arch. v. Pflüg.*, 1874, t. VIII, p. 347. —Harless, Abhandl. d. K. Acad. Physik, 1858, t. XXXI.—Heidenhain, *Arch. v. Pflüg.*, 1871, t. IV, p. 435.—Hering, *Neurol. Centralbl.*, Leipzig, 1897 ; *Arch. f. exper. Path. und Pharm.*, 1898.—Marcacci, *Arch. p. le sc. med.*, Torino, 1882, t. V, p. 283.—Mott et Sherrington, *Proc. Roy. Soc.*, 1895.—Sherrington, *Proc. Roy. Soc., London*, 1893.—Steinmann, *Bull. Acad. imp. d. sc. St.-Pétersb.*, 1871, t. VII.—Stilling, *Arch. f. physiol. Heilk.*, Stuttgart, 1842.

Motor Roots, Functional Localizations, Constitution of the Plexuses.—Bert et Marcacci, *Lo Sperimentale*, 1881 ; *Biol.*, 1881.—Ferrier et Yeo, *Proc. Roy. Soc.*, 1881.—Forgue, Thèse Montpellier, 1893.—Forgue et Lannegrace . . . Distrib. dans les muscles, *C. R. Ac. sc.*, 1884, t. XCVIII, pp. 685 et 1068.—Herringham, *Proc. of Roy. Soc.*, London, 1886.—Paterson, *Journ. of Anatomy*, 1894 et 1899.—Polimanti, *Arch. ital. biol.*, 1895, t. XXIII, p. 333.—Russel, Plex. brach. chien, *Philosoph. Transact.*, 1892.—Sherrington, Plex. lombo-sacré, *Journ. of Phys.*, 1892, p. 708.—Simon, Disserta., Strasbourg, 1892.

Cranial Nerves.—Voyez spécialement Cl. Bernard, Leçons sur le syst. nerv.—Longet, Traité de physiol., édit. 3—Magendie, *Journ. de Phys.*—W. H. Gaskell, *Journ. of Phys.*, 1889, p. 153.—His, Morph. Betracht. der Kopfnerv., *Arch. f. An. und Phys.*, 1887.—Kupffer, . . . Entwickel. . . . Verh. d. anat. Gesellsch., 1891.—Bulloch, *Brain*, 1894.

Motor Nerves of the Eyes.—Adamuk, *Centralbl.*, 1870.—Bruce, Article de Marinesco, *Sem. med.*, 1896.—M. Duval, Origines, mouvem. associés, *Biol.*, 1878 et 1879 ; *Journ. de l'anat.*, 1880.—Duval et Laborde, *Journ. de l'anat.*, 1880.—Francès, Essai sur la paralysie de la 3 paire, 1854.—Laborde, Procédé d'arrachement, *Biol.*, 1879 et 1896 ; *Journ. de l'anat.* 1880.—Landouzy, *Arch. gén. méd.*, 1878 ; *Biol.*, 1879.—Parinaud, Paralysie dissociée, 3 paire, *Biol.*, 1880.—Stuelp, *Graefes Arch.*, XLI.

Ciliary Nerves and Ganglion ; Accommodation.—Boucheron, N. ciliaires, *Biol.*, 1891 et antér.—Hensen et Wolckers, *Arch. de Gräfe*, 1878.—Iegorow, *Arch. slaves de biol.*, 1886 et 1887.—Schwalbe . . . Gangl. cil., *Iena Ges.* et *Iena Zeit.*, 1878 et 1879.

Trigeminal Nerve.—Althaus, *Arch. f. klin. Med.*, 1870.—Bastianelli, *R. acad. med. d. Roma*, 1895.—Bellingeri, De nervis faciei, 1818. Debierre et Lemaire, *Biol.* 1895.—Eschricht, *Journ. de Magendie*, t. IV.—Hirschberg, *Berlin. klin. Woch.*, 1868. —Guttmann, *Berlin. klin. Woch.*, 1868.—Krueckmann, Sensib. de la cornée, *Graefes Arch.*, vol. XLI.—Laffont, Trij. fac. symp. chez oiseau, *C. R. Ac. sc.*, 1885, t. CI. p. 1286.—Long et Egger, Paralysie chez l'homme, *Arch. phys.*, 1897, p. 905.—Lugro, Rac. desc., *Arch. ital. biol.*, 1895.—Prevost, Fonct. gust. du lingual, *Arch. Phys.*, 1873. pp. 253 et 375.—Quenu, Tic doul. *Gaz. des hôp.*, 1894.

Vaso-motor Functions.—Dastre et Morat, *Biol.*, Rech. sur le syst. nerv. vaso-moteur, Paris, Masson.—Jolyet et Laffont, *Biol.*, divers.—Laffont, *Biol.*, divers.—Vulpian, *C. R. Ac sc.*, 1885, t. CI, p. 981.

Trophic Disturbances.—Antona, *Il Policlinico*, 1894.—Doyen, Extirp. gangl. de Gasser, *Arch. prov. de chir.*, 1895.—Krause, 24 congr. chirurg. allem. 1895.—Léonard, Thèse Paris, 1894.—Marinesco et Sérieux, *Arch. Phys.*, 1893, p. 455.—Ramier, Plexus nerv. de la cornée, *C. R. Ac. sc.*, 1879, t. LXXXVIII, p. 1087.—Schmidt, *Deutsch. Zeitsch. f. Nerv. heilk.*, 1895.

Trophic Disturbances of the Eye.—Cl. Bernard, *Biol.*, 1874.—Bezold, *Deutsch. Klin.* 1867.—Hippel, *Arch. f. Ophthalm.*, 1867.—Magendie, *Journ. de Phys.*, t. IV.—Messner, *Zeitsch. f. rrat. Med.*, 1867.—Ranvier, Anatomie de la cornée.—Schiff, *Zeitsch. f. rrat. Med.*, 1867.—Snellen, *Nederl. Tij. voor Geneesk.*, 1864 ; De vi nervorum in inflammationem, 1857.

Intra-ocular Tension.—Adamuk, *Wien. Acad.*, 1869.—Hippel et Grunhagen, *Arch. f. Ophthalm.*, 1868, 1869.—Hirschberg, *Centralbl.*, 1875.

Trophic Disturbances ; the Ear.—Gellé, *Gaz. Méd.*, 1878.—Hagen, *Arch. f. exper. Path.*, 1879.

Vaso-motor and Adaptive Function ; Vision, Audition, etc.—Doyon, Vaso-mot. retine, *Arch. Phys.*, 1891.—Eckhard, *Centralbl. f. Phys.*, 1892, p. 129.—Jolyet et Laffont, *C. R. Ac. sc.*, 1879.—Laffont, *Biol.*, 1880.—Morat, Ganglion du muscle du marteau,

Congrès de Liège, 1892.—POLITZER, *Wurzb. nat. Zeit.*, 1861 ; *Arch. f. Ohrenheilk.*, 1876.—PRÉVOST, Gangl. sphéno-palatin, *Arch. Phys.*, 1868, pp. 7 et 207.—VOLTOLINI, *Arch. f. path. An.* 1875.—VULPIAN, *C. R. Ac. sc.*, 1885, pp. 851, 981, 1037, 1448.

Facial.—BEAUNIS, *Biol.*, 1887, p. 205.—BÉRARD, Journ. des connaiss. méd., 1834-35.—CL. BERNARD, *Gaz. méd.*, 1857.—BIKELES, Dégén. asc., *Wiener med. Presse*, 1893.—BOCHEFONTAINE, Procédé de section intracran., *Biol.*, 1879.—BROWN-SÉQUARD, *Gaz. méd. Biol.*, 1849 et 1869.—CHANTRE, *Arch. Phys.*, 1891, p. 629.—DEXLER, Paralysie chez le cheval, dyspnée par occlusion des narines, *Wiener med. Presse*, 1896.—GOEDECHENS, N. facialis physiol. et path., 1832.—HALLOPEAU, Trajet intracérébr. ram. supér., *Biol.*, 1879, p. 244.—LAFFAY, Sect. intracran., *Arch. Phys.*, 1897, p. 498.—LUI, Paralysie . . . mouvem. des paupières, *Archivio per les sc. med.*, 1884.—VULPIAN, *C. R. Ac. sc.*, 1878 ; *Biol.*, 1861 et 1879.

Nerve of Wrisberg : Geniculate Ganglion.—BIRMINGHAM, *Journ. of An. und Phys.* 1895 —CANNIEU, *C. R. Ac. sc.*, 1895, t. CXX, p. 880, et *Revue de laryngol.*, 1894.—CHIARUGI, *Monit. zool. ital.*, 1896.—FRORIEP, Corde tymp., *Anat. Anz.*, 1887.—PENZO, *Anat. Anz.*, 1895.—VULPIAN. *C. R. Ac. sc.*, 1885, t. CI, p. 1037 ; 1886, t. CIII, p. 671.

Chorda Tympani : Vaso-motor Functions ; Gustatory Functions.—BLAU, *Berlin. klin. Woch.*, 1879.—CARL, Fonct. gustat., *Arch. f. Ohrenheilk.*, 1875.—LUSSANA, Sui nervi del gusto, *Gaz. méd. ital.*, 1871.—STICH, *Ann. d. Charité Frank.* z. Berlin, 1857.—VULPIAN, *C. R. Ac. sc.*, 1872, et *Biol.*

Glosso-pharyngeal.—BIFFI et MORGANTI, *Ann. univ. di med.*, 1846.—CADMAN, Glossophar. vague et spinal, *Journ. of Phys.*, 1901, 1, p. 42.—ISERGIN, *Arch. f. An. und Phys.*, 1894, p. 441.—KATZENSTEIN, *Arch. f. An. und Phys.*, 1894, p. 192.—KRONECKER et MELTZER, *Arch. f. An. und Phys.*, 1883, suppl. p. 328.—LUSSANA, Nerfs du goût, *Arch. Phys.*, 1871, 2, pp. 150, 334, 522.—MARINESCU, Innerv. drüs. zungenbasis, *Arch. f. An. und Phys.*, 1891, p. 357.—MUCHIN, *Centralbl. Nerv. heilk.*, 1893.—POPE, *Brit. med.*, 1889, I.—SANDMEYER, *Arch. f. An. und Phys.*, 1895, p. 269.—VINTSCHGAU et HÖNIGSCHMILD, *Arch. v. Pflüg.*, 1877, t. XIV, p. 443.—VULPIAN, *C. R. Ac. sc.*, 1880, t. XCI, p. 1032.

Pneumo-gastric.—ARTHAUD et BUTTE, Du nerf pneumogast. physiol. norm. et path., Paris, 1892.—VAN KEMPEN, Thèse Louvain, 1842.

Respiration : Lung.—D'ARSONVAL, Thèse Paris, 1877.—BEER, *Arch. f. An. und Phys.*, 1892, suppl., p. 101.—P. BERT, Leçons sur la respiration.—BORIS BIRUCKOFF, *Arch. f. An. und Phys.*, 1899, p. 525.—BROWN-SÉQUARD, *Arch. de Phys.*, 1882 à 1891.—G. BROWN, *Journ. of Phys.*, t. VI, 1885.—CONSIGLIO, *Arch. ital. de biol.*, 1892, t. XVII, p. 49.—COUVREUR, Circul. pulmon. gren., *C. R. Ac. sc.*, 1889, t. CIX, p. 823.—DOYON, *Arch. Phys.*, 1893, p. 93.—I. GARD, *Arch. f. An. und Phys.*, 1881.—GRÉHANT, Éch. resp., *Biol.*, 1882.—FRÉDÉRICQ, Traité de physiologie, *Bull. Ac. roy. Belg.*, 1879.—KOHTS et TIEGEL, *Arch. v. Pflüg.*, 1876, t. XIII, p. 84.—HERING et BREUER, 1868.—ROSENTHAL, *Arch. f. An. und Phys.*, 1862 à 1881 ; *C. R. Ac. sc.*, 1861.—SCHIFF, *Arch. v. Pflüg.*, 1871, t. IV, p. 226 ; *C. R. Ac. sc.*, 1861 ; Lehrbuch. Musk. and Nerv. physiol., 1858-59.—SPALLITA, *Arch. ital. de biol.*, 1891, t. XV, p. 376.—STEFANI et SIGHICELLI, *Arch. ital. de biol.*, 1889, t. XI, p. 143.—TREVES, *Arch. ital. de biol.*, 1897, t. XXVII, p. 169.

Laryngeal Nerves.—BEDOR, Thèse Paris (ictus laryngé), 1895.—BODDAERT, *Arch. Phys.*, 1862, p. 443.—CAGNEY, Abduct. et adduct., *Deutsch. Zeitschr. f. Nervenheilk.*, 1895.—DONALDSON, *Americ. Journ. of the med. sc.*, 1886.—EXNER, *Arch. f. ges. Phys.*, 1893 ; *Arch. f. An. und Phys.*, 1891.—FR. FRANCK, *Journ. de l'anat.*, 1877, p. 560 ; Anast. de Galien, *C. R. Ac. sc.*, 1879.—KATZENSTEIN, *Arch. f. An. und Phys.*, 1894 à 1899.—KRISHABER, *Biol.*, 1880.—HEDON, Élém. vaso-dilat. et sécrét., *C. R. Ac. sc.*, 1896, t. CXXIII, p. 267.—HOWELL et HUBER, *Journ. of Phys.*, 1891, p. 5.—JEAN, *Soc. anat.*, 176.—LEGALLOIS, Œuvres, 1830.—LIVON, Act. des récurrents, *Biol.*, 1890 ; *Arch. Phys.*, 1890, p. 587, et 1891.—LOEWY, *Arch. f. d. ges. Phys.*, 1893.—MASINI, *Acad. de Gênes*, 1893.—H. MUNK, *Arch. f. An. und Phys.*, 1891, pp. 175 et 542, et 1894, p. 192.—NEUMANN, *Centralbl. f. med. Wiss.*, 1893.—ONODI, Muscle crico-thyroïdien, *Revue de laryng., otol. et rhinol.*, 1893.—PINELES, *Centralbl. f. Phys.*, IV, No. 24, p. 741.—RAUGÉ, *Arch. de Phys.*, 1892.—TODD et GARDNER, *Arch. gén. méd.*, 1853.—ZUNTZ, *Arch. f. An. und Phys.*, 1892, p. 163.

Heart.—ARLOING, Tétanos du myocarde, *Arch. Phys.*, 1893, p. 103, et 1894, pp. 85 et 163.—ARLOING et TRIPIER, *Arch. Phys.*, 1871, 72, 73.—FRANÇOIS FRANCK, *C. R. Ac. sc.*, 1880 ; Action antitonique, *Arch. Phys.*, 1891.—A. GAMGEE, Excit. alternat. . . . *Journ. of Phys.*, 1879-80, vol. 1, p. 39.—GASKELL, Changem. électr. . . ., *Journ. of Phys.*, 1886, p. 451.—GURBSKI, Sensib. du cœur, *Arch. v. Pflüg.*, 1872, t. V, p. 289.—LABORDE, *Arch. Phys.*, 1888.—LAULANIÉ, Effets second., *C. R. Ac. sc.*, 1889, t. CIX, pp. 377 et 407.—LEGROS et ONIMUS, *C. R. Ac. sc.*, 1872, t. LXXV, p. 1192.—W. MILLS, *Journ. of Phys.*, 1884, t. V, p. 359.—MUNZEL, *Arch. f. An. und Phys.*, 1887, p. 120.—ONIMUS, *C. R. Ac. sc.*, 1876, t. LXXXIII, p. 988.—H. SEWALD et F. DONALDSON, *Journ. of Phys.*, 1880-82, vol. III, p. 357.—STEFANI, Act. protect., *Arch. ital. de biol.*, t. XXIII, p. 175.—STEWART, Températ., *Journ. of Phys.*, 1892, p. 59.—TARCHANOFF, *Arch. Phys.*, 1875, p. 498.—

TARCHANOFF et PUELMA, Excit. alternat. des deux vagues, *Arch. Phys.*, 1875, p. 757.—ZANDER, Oiseaux . . ., *Arch. v. Pflüg.*, 1879, t. XIX, p. 263.

Pharynx, Œsophagus, Stomach and Intestine.—CL. BERNARD, Sécrétion . . ., *Bull. Acad. de méd.*, 1852.—V. BRAAM HOUCKGEEST, Mouvements . . ., *Pflüg. Arch.*, Bd. VI, p. 266, et Bd. VIII, p. 163.—CHAUVEAU, N. pneumogast. ag. excit. contr. œsophagiennes, *Journ. Phys. de l'homme et des animaux*, t. VI, 1862 ; Excitation des nerfs crâniens, *Ibid.*—EHRMANN, Intestin. . . ., *Wiener med. Jahrb.*, 1885.—ESPEZEL, Innerv. œsoph., *Journ. de Phys. et pathol.* 1901.—LONGET, Mécan. occlusion de la glotte, déglutition, *Arch. gén. méd.*, 1841.—MORAT, *Lyon méd.*, 1882.

Liver.—CL. BERNARD, Leçons sur la physiol. expérim., 1854, t. I, p. 336.—DOYON, Voies biliaires, thèse Fac. sc. Paris.—FILEHNE, *Centralbl. f. Med.*, 1878.—HEIDENHAIN *Stud. Phys. Inst. z. Breslau*, Heft 2 und 4.—LAFFONT, *C. R. Ac. sc.*, 1880 ; *Journ. anat. et Phys.*, 1880.

Kidney, Bladder.—ARTHAUD et BUTTE.—MASIUS, *Bull. Ac. roy. Belg.*, 1888.—OEHL, *C. R. Ac. sc.*, 1865.—G. SÉE et GLEY, Azoturie . . ., *Biol.*, 1888.—VULPIAN, Vasomoteurs, t. I.

Spleen.—BOCHEFONTAINE, *Arch. Phys.*, 1873.—OEHL, *Schmidt's Jahrb.*, 1869.—TARCHANOFF, *Arch. Pflüg.*, 1873.

Spinal Accessory Nerve.—TH. BISCHOFF, Nervi accessor, Will. an. et phys., Heidelberg, 1832.—BISCONS et MOURET, *Biol.*, 1894.—CL. BERNARD, *Arch. gén. méd.*, 1844 ; Leçons sur le syst. nerveux.—LONGET, *Gaz. méd.*, 1841.—MIRTO et PUSATERI, *Riv. di pathol. nerv. clement.*, 1896.—SCARPA, De gangliis nervorum . . ., H. Weber, Milano, 1831.—W. SCHLOTTMANN, *Deut. Zeitsch. f. Nervenheilk.*, 1894.

Hypoglossal Nerve.—DIELOFF, *Clin. neuro-psych.*, 1896.—DUVAL, Noy. d'origine différents pour la parole et pour la déglutition, *Biol.*, 1879, p. 239.—FÉRÉ, Spasme des muscles . . ., *Biol.*, 1827, p. 239.—LAFFONT, *Année méd.*, 1883.—WERTHEIMER, Anastom. br. descend., *Biol.*, 1884, p. 589.

CHAPTER II

PRIMARY SYSTEMATIZATIONS

SENSATION and motion are present in us in forms which are extremely finely graduated. Those of these forms which correspond to the idea ordinarily held of sensation (conscious sensation) and of movement (voluntary movement) are the most elaborated, and also the most complex. They are founded on more elementary associations both of sensibility and of movement than we can recognize. We will examine three of them : in the first place, *reflex action* is that which demonstrates to us in its greatest simplicity the transformation of a sensory into a motor excitation, movement being the end which is aimed at. Hence it is, further, a phenomenon which often intervenes (perhaps even habitually to a certain degree) in the reflex act which it complicates and to which it gives a novel aspect and physiognomy. In the second place, *inhibition or arrest*, a phenomenon in virtue of which the sensory excitation does not exert its immediate effect, but, on the contrary, suspends, postpones the motor effect, and in this way increases its variety. Lastly, it is the inverse bond existing between movement and sensation which permits them to maintain themselves mutually in the organism, in an automatic fashion, thus preserving the impulse in its interior, indeed, in the interior of the nervous system, by a genuine *circulation* comparable to that of matter and of energy.

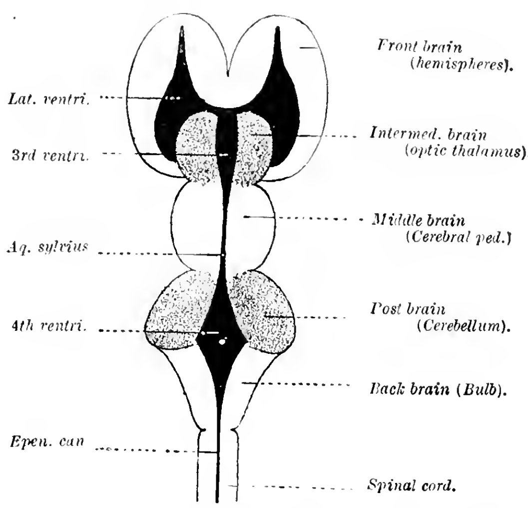


FIG. 97.—The cerebral vesicles in the embryo (diagram copied from Gegenbaur).

Origin of the nervous system.—The nervous system is rendered necessary by the complications of the organization of animals arranged in an ascending series. In proportion as the functions become more numerous through differentiation

by the division of labour, a special tissue is developed, whose duty it is to harmonize these different portions and to maintain their organization.

In the freshwater *hydra*, the body wall, proceeding from the exterior to the interior, is divided into two epithelial layers, one external and the other internal. Between the two is a sort of intermediate layer of contractile nature. This interposed layer is not formed of independent elements, but the fibres, apparently muscular, which compose it are attached by a bridge of continuous substance to the epithelial elements of the superficies. The excitations received by the external surface of these latter are thus transmitted by continuity of substance to their deep portion, which is muscular, or at least contractile. Those tracts, which connect two functionally differentiated portions of a similar element, may be looked upon as the preliminary sketch of a nervous tissue.

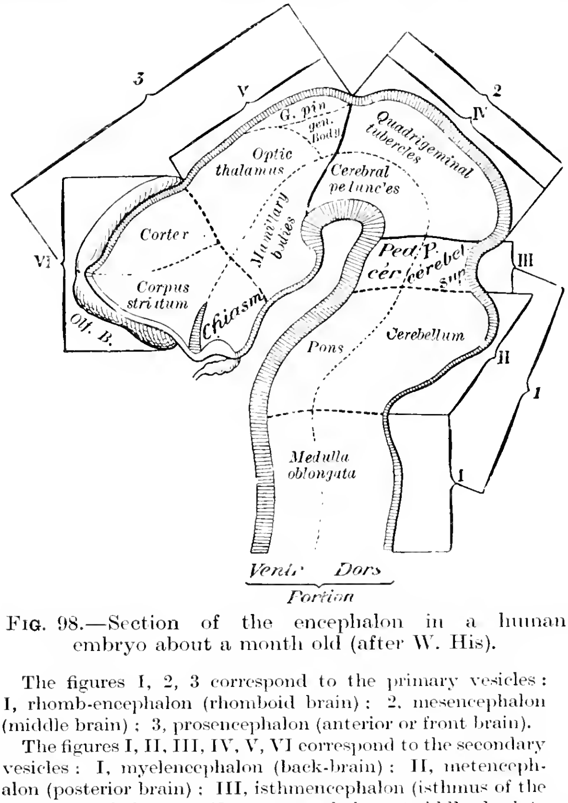


FIG. 98.—Section of the encephalon in a human embryo about a month old (after W. His).

The figures I, 2, 3 correspond to the primary vesicles: I, rhomb-encephalon (rhomboid brain): 2, mesencephalon (middle brain); 3, prosencephalon (anterior or front brain).

The figures I, II, III, IV, V, VI correspond to the secondary vesicles: I, myelencephalon (back-brain): II, metencephalon (posterior brain); III, isthmencephalon (isthmus of the rhombencephalon); IV, mesencephalon (middle brain); V, diencephalon (intermediate brain): VI, telencephalon (terminal brain).

In other animals whose organization is still very rudimentary, we find this tissue isolated from other tissues, forming a rudimentary system. Such is the nervous system of an *ascidian*, formed of a ganglion which is connected by structures or by nerves properly so called to organs, some receptive of stimulation, others which perform functions. This little elementary system is a reflex arc similar to innumerable others found in superior animals, but in them coordinated amongst themselves and organized into a series of complicated systems of which they form the constituent elements.

Its development.—The nervous system in the *vertebrata* is obvious from the very earliest days of development. It takes origin in the *ectoderm*. In the first instance it presents itself under the form of a thickened band, *neural plate* or *neural furrow*. This furrow is transformed into a groove (*medullary or neural groove*) which is orientated in the direction of the long axis of the body. Its borders project upwards, unite, and thus form the *medullary or neural canal*. This canal becomes separated from the rest of the ectoderm, which closes below it. It already represents the spinal cord with its ependymal canal. At its anterior extremity this canal forms three dilatations, which are the *cerebral vesicles* (*anterior, middle and posterior*), which will give rise to the encephalon.

The division of the anterior and posterior vesicles, each of which forms two new vesicles, increases to five the number of *secondary* vesicles, and thus produces *an anterior brain, an intermediate brain, a middle brain, a posterior brain, and an after brain.* The primitive middle vesicle becomes the middle brain. The anterior brain (the most anterior of the secondary vesicles) becomes very considerably developed in man. It divides on the median line and gives origin to the two hemispheres separated by the interhemispherical fissure. All these vesicles and the cavities which they contain assume very different configurations, and give rise to new formations.

The portion of the primitive canal which corresponds to the middle brain becomes relatively contracted, and forms the aqueduct of Sylvius, which communicates posteriorly with an enlarged portion of the after brain, the fourth ventricle itself being continuous with the ependymal canal of the spinal cord. The aqueduct of Sylvius is continuous in front with the third ventrical (of the intermediary brain), and in this way communicates with the lateral ventricle hollowed out in each hemisphere. According to the nomenclature of His, the posterior primitive vesicle includes yet another division, *the isthmus of the rhombencephalon,* which increases the number of secondary divisions to six.

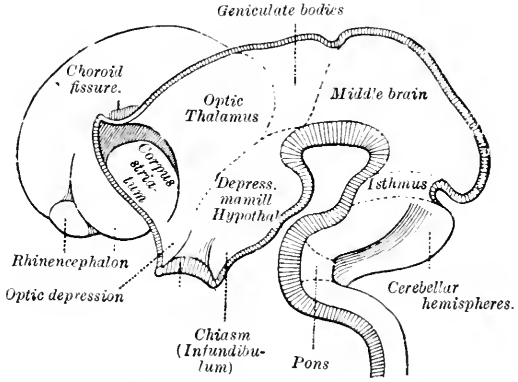


FIG. 99.—Section of the encephalon in a human embryo of five weeks (after W. His).

More advanced development of the different formations arising from the cerebral vesicles, and especially the hemispheres.

The wall of the neural canal is at first formed of a single row of cells which constitute its thickness. Yet, alongside of these epithelial cells, which will remain in position and will become the elements of the ependyma, others are also present, which are in process of caryocinetic division, to which His, who observed them, has given the name of *germinative cells.* At a given moment, which varies for each of them, these latter cease to multiply and become *neuroblasts,* that is to say, cellular elements giving rise to *neurons.* Through the development of their prolongations beyond the medullary cylinder, certain of them proceed to join the muscles. By thrusting out these prolongations towards the interior both of the brain and the cord, the elements of which they are formed enter into relation the one with the other. It remains for the connexion of the central parts with the skin and the organs of sense to be established. This is effected by elements which have remained outside these masses at the time of their formation.

During the period in which the neural furrow is hollowed out, its borders present a crest (*neural or ganglionic crest*); it is from this double crest, which is first of all united and then dissociated, that the *spinal ganglia* take their origin. The cells of these latter join the skin on the one hand, and on the other the spinal cord, and in this way the cycle of excitation is completed. In the invertebrata (and also in the vertebrata as regards the organs of sense other than touch) these cells remain scattered at the periphery in contact with the ectoderm and are joined to the grey axis by their axons.

A. COMMUNICATION OF STIMULATION; REFLEX ACT

The reflex act is of all systematic nervous actions the simplest. Theoretically, it requires the participation of two nerve elements, one of which transmits to the other the impulse which it has itself received. The existence of this simple connexion between certain neurons is easily demonstrated, especially between the elements of the posterior roots and those of the anterior roots of the spinal cord.

If, for example, in a frog, a small segment of the spinal cord corresponding to a nerve pair (metameric segment) is isolated between two sections, and if then the sensory nerve be stimulated either directly or by irritation of the skin, the muscles to which the motor nerve is distributed will respond by a contraction. The impulse starting in the skin is, as is said, reflected by the spinal cord in such a way as to return near to its point of departure.

Historical.—Long ago it had been remarked that certain movements which were altogether involuntary ensued as a response to sensitive or sensorial excitations. The phenomenon had been observed and recorded by Montaigne and Descartes; it appears that Astruc had already described it as "*reflex*" (1743); but, according to Longet, it is to Prochaska (1784) that the first experimental data concerning the question are due. He was the first to observe the movements of response of the decapitated frog when its skin is irritated; he attributed these movements to a phenomenon which was centred in the spinal cord, and which he designated by the name which it has since preserved: "*impressionum sensoriarium in motorias reflexio*"; he saw quite clearly the simple relation which exists in this case between sensation and movement. He compared to these facts the involuntary acts which are observed in man, such as winking of the eyelids, sneezing, coughing, vomiting, following a sensorial or sensory impression which is rather active and unexpected or extra-functional, and also the movements of the limbs induced by irritations of the skin during sleep or in apoplectic patients, as being movements, so to speak, independent of consciousness and of the will.

Legallois reproduced these facts and these observations without recognizing their nature. His experiments confirm the reflex or *intrinsic power* of the spinal cord which he observed in mammals after section of the bulb by effecting pulmonary insufflation. Lallemand observed facts of this kind in anencephala. Calmeil equally insisted on the function of motor co-ordination of the spinal cord as being independent of that of the encephalon. J. Müller and Marshall-Hall extended these data and applied them to the explanation of a large number of pathological phenomena.

Extension of the phenomenon.—Inasmuch as the muscular movement is the most visible of any in the organism, it was only natural that it should at first serve as the chief characteristic of the reflex phenomenon. But when Cl. Bernard and Ludwig had extended the action of the nervous system to the vessels and glands, the area of reflexes took a new extension and became in a way generalized. As, on the other hand, the vaso-motor and secretory nerve influence is always involuntary, the reflex act, from being in some degree an exceptional phenomenon as it at first appeared, became the primary and essential form of the function of innervation. Voluntary movement is nothing more than the elaborated form of reflex action; muscular movement is itself merely a differentiated form of organic movement usually hidden and invisible.

1. **Localized reflex actions.**—Masius and Vanlair, by the method of systematic section of the myelaxis, have proved *that each segment of the spinal cord, corresponding to a nerve pair, can act as a point of reflection of the impressions from the sensory root to the corresponding motor root.* Each of these segments is limited by two planes, the posterior passing immediately behind the insertion of the corresponding roots, the anterior immediately behind the roots of the pair situated in front. It is in every case, with this limitation as regards the segments, that reflection is most favourably observed. The lumbar enlargement of the spinal cord is very well adapted for this investigation. The segment corresponding to the tenth pair of spinal roots can be perfectly isolated from the others, the segment of the seventh pair equally so ; it is more difficult to dissociate the eighth and the ninth segment, inasmuch as the sensory areas of these two nerve pairs are less distinct.

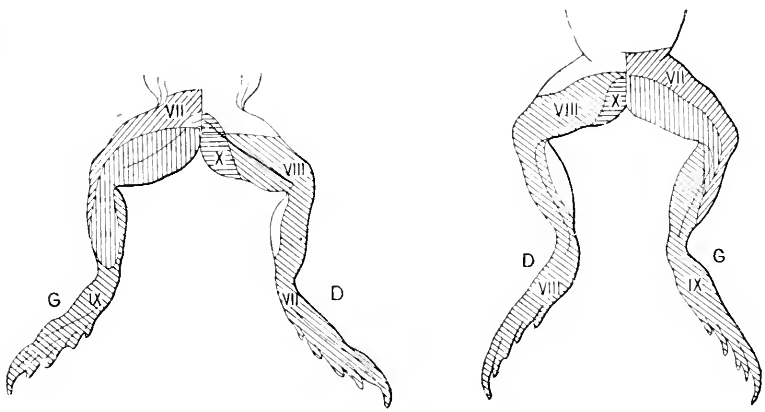


FIG. 100.—Cutaneous areas of the VIIth, VIIIth, IXth and Xth nerves of the frog. On the right front view and on the left back view of the animal. D, right limb : G, left limb. These areas are determined by the reflex responses to the stimuli brought to bear upon them.

These authors have, indeed, commenced by determining the cutaneous territories corresponding to the sensory roots of each nerve pair by separately cutting these roots, in order to ascertain the corresponding area of anæsthesia. Then they experimented on these areas, thus delimited, in order to produce excitation. The reflex movements are more marked when the sensory receptive apparatus, which is adapted to the functional stimulation, is acted upon than when the stimulus is brought to bear upon the sensory nerve itself.

Anatomical data. Connexions between elements.—Anatomy, thanks to the employment of new methods (method of Golgi), has demonstrated the existence of these connexions. In a section of the spinal cord, *certain collaterals of the*

posterior roots, which proceed in the grey matter in order to come in contact with the dendrites of the anterior roots, may be followed (Cajal). Thus the reflex arc is formed by a system of at least two nerve elements, connected consecutively, but this association is not so simple as is commonly supposed. By observing, indeed, in a spinal segment artificially isolated as above, that the sensory root corresponds to a motor root, it might be supposed that each fibre of the one corresponds in the same way to a fibre of the other; but this is not the case. The field of distribution of a sensory neuron corresponds to several motor neurons (certain of them, indeed extend to a great length of the spinal cord). Conversely, the initial arborizations of the motor neurons, although occupying a much less extended area, enter into relationship with several sensory neurons.

There is reciprocal, although unequal, overlapping of the areas by which these contacts are effected. *The impulse conveyed by a single sensory element is transmitted, in a certain order, to several motor elements, and the impulse, simultaneously*

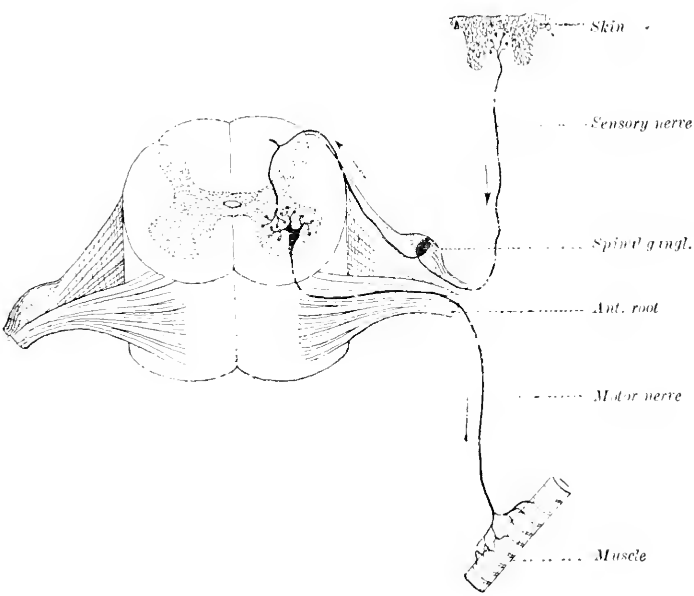


Fig. 101.—Elementary reflex arc.

Course of a sensory impression and a motor impulse passing through the same level of the spinal cord.

conveyed by several sensory elements, may converge on a single motor element. On account of similar connexions, the impulse undergoes a special arrangement in the grey matter which gives to it an entirely new form of aggregation. It is, as we say, transformed.

Elements of association.—Not only have the two neurons known as sensory and motor these complicated connexions, but it is not proved, even for the performance of the most simple reflexes, that these conditions suffice, and it is necessary to take into account elements superadded to the preceding. Intermixed with the terminal and initial arborizations of the neurons thus joined together are ramifications of short cells discovered by Golgi; these elements are neurons running a short course, which would seem to serve as a means of association between the preceding. Hence an impulse, in order to proceed from a sensory

to a motor nerve, follows routes, some of which are direct, others roundabout, each of which in its own way contributes to give to the process of stimulation a necessarily complex aspect.

Forms of reflex movement varied according to the point of departure, or the intensity of stimulation.—It has been shown experimentally that irritation of different areas of the skin may produce varied reflex movements of the different articulations (Sanders-Hezn) ; thus the difference in intensity of the stimulation will give rise, when weak, to a movement of flexion ; when strong, to a movement of extension of the hind limb (Vulpian).

2. **Typical form.**—Etymologically, the word *reflex* signifies "return of the impulse towards its point of departure by passing through that which is known as a centre." The ganglia of the great sympathetic, the grey matter of the spinal cord, furnish simple examples of this phenomenon. But, according as the impulse penetrates more or less deeply into the central masses of the nervous system, according as it reaches the medulla oblongata, the basal ganglia, or even the cerebral cortex, the reflex act becomes continually more complicated, without ceasing to be fundamentally a phenomenon of the communication and transmission of the impulse through a chain of elements. Hence there is, between the simplest and the most complicated actions of the nervous system, a continuity which causes the second to take origin from the first by an insensible gradation. This is why it is said that the function of the nervous system, regarded as a whole, as well as in detail, is merely a reflex phenomenon. The reflex act is, under any circumstances, the simplest image which we can employ in order to characterize this totality of action.

Ordinary sense of the word.—Yet, in current language, the word *reflex* is used to designate the simplest, the most uniform, and the most circumscribed nervous acts, both as regards time and space, as opposed to those which their complication, their contingency, their extension in the nervous system and their duration remove from the primitive type in which they originate. And there is another reason for this.

3. **Conscious, subconscious and unconscious reflexes.**—The simple, ordinary reflex has the aspect of a purely mechanical movement of transmission. Consciousness and spontaneity appear to be totally absent from it ; on the other hand, this spontaneity and this consciousness seem to characterize the actions which require the intervention of the superior portions of the nervous system, and especially of the cerebral cortex. Hence the reflex act has been, and is, opposed to the voluntary act. In practice, however, this opposition is based on the condition that it is not regarded as absolute.

Just as, in the order of movement, we proceed from the simple

reflex act, from the ganglionic or spinal reflex, to the most complex cerebral act, so, from this extremely perfected act, we re-descend, in the psychical order, without solution of continuity, to the nervous act, the fundamental base of all the others, and we meet with traces of this consciousness and of this choice, which only appear in their plenitude and in a marked form in those superior systematizations which are effected in the brain. Three chief degrees may be distinguished in this succession, corresponding (1) to the reflex act, (2) to the instinctive act, (3) to the voluntary act.

4. **Elementary reflex.**—As often as the impulse is communicated from one nerve element to another which follows it, there is reflexion of this impulse in the most general sense of the word, whatever may be its point of departure and its point of termination. In this sense it is sometimes said that the impulse is reflected from the posterior roots to the tracts of the spinal cord, in conscious impressions, and from these latter to the anterior roots in voluntary movements, exactly as it is from the posterior roots to the anterior roots in the reflexes properly socalled.

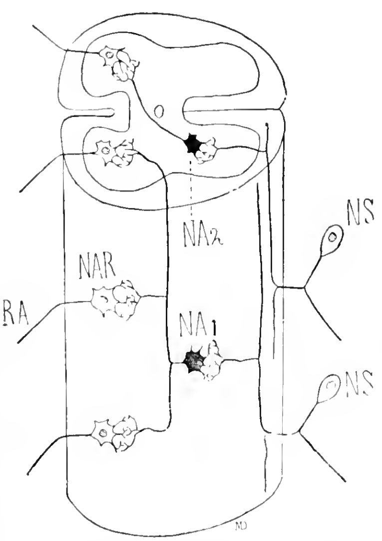


Fig. 102.—Elements of association (in heavy type), overlapping of the polar fields (after M. Duval).

NS, sensory neuron; NAR and RA, radicular motor neuron; NA[1], automere neuron of association (situated in the same half); NA[2], hetromere, neuron of association (passing from one half to the other of the spinal cord).

Centre of reflection.—The locality in which the impulse changes its route and is reflected is usually called the *centre of reflection*. This region is clearly that in which the terminal arborizations of the first neuron reach the initial arborizations of the second neuron; in other words, the site of reflection is at the union of the two neurons, on the hypothesis of an elementary reflex. In proportion as elements of association are superadded to this primitive system, the site of reflection assumes a more complicated aspect, like the system itself. The word *centre*, so often made use of, is, as is obvious, much diverted from its etymological meaning.

5. **Experimental data.**—Anatomical data, incomplete as they are, have nevertheless shown us above according to what complex laws the *connexions* of the nerve elements, which act in a reflex manner,

are effected. Physiology, for its part, shows us what *transformations* the impulses undergo from the fact of their passage through the grey matter, where these connexions are carried out.

We will now consider a small reflex system formed of a segment of the spinal cord; this system is supplied with its sensory and motor nerves, which have preserved their relations with the peripheral organs (muscles and skin); stimulations may be brought to bear on the skin, on the sensory nerve, on the motor nerve, or on the muscles, and all will be followed by different results; but it is especially when the sensory and motor nerve are stimulated comparatively that the results differ and are most instructive. This stimulation induces in the nervous path which leads to the muscle two impulses, the one above, the other below the grey matter, or site of association.

Retardation of the impulse.—A first very obvious result is the retardation which attends the transmission of the impulse in its progress through the grey matter. This retardation is, indeed, considerable, to judge by the results of experiments on animals. In the frog it may amount to a fourteenth of a second. It has been frequently estimated in man in certain prominent reflexes, such as the patellar reflex. As regards the transmission of the impulse from nerve to nerve, it represents a latent period analogous to that observed in the transmission of an impulse from nerve to muscle.

Intensity.—In order to obtain the same amount of contraction, the intensity of the stimulation must often vary considerably, according as it is applied to the sensory or motor nerve. Hence there is, in this respect also, an alteration which takes place in the site of transmission.

To put the matter more clearly, the results of the stimulation of the motor nerve present a constancy (at least relative) which is not present in the same degree in those which follow the stimulation of a sensory nerve. This is expressed by saying that *reflex excitability is variable*. If may be inferred, indeed, that the conditions on which this variability depend must be sought in the locality where the sensori-motor impulses are associated, and not elsewhere. In principle, the excitability of the sensory nerve should have the same fixity as that of the motor nerve; but the grey matter, according to circumstances, is hardly ever consistent with itself. As a result of the changes of which it is the seat, there will be between the effects of stimulation above and below the site of reflection a predominance of results: sometimes of sensory stimulation, which is rare; sometimes of motor stimulation, which is the rule; exceptionally there will be equality.

Absorption and restitution.—To judge by the crude results of ex-

periments, the ordinary effects of sensory excitation are markedly a loss of its intensity in its passage through the grey matter. This loss is probably more apparent than real. In any case, it must not be concluded that, in the normal exercise of function, matters are necessarily arranged in this fashion. The stimuli which we cause to penetrate artificially the trunk of a motor or sensory nerve are not the exact equivalents of those which it receives, by its dendrites, from

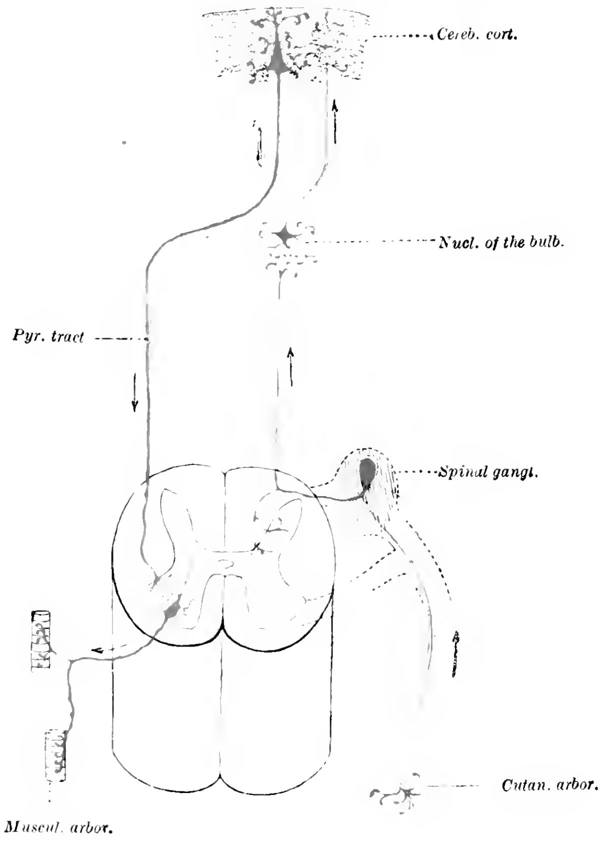


FIG. 103.—Cerebral reflex permitting the succession of several elementary reflexes. Sensory paths in blue; motor paths in red.

the special organs whose duty it is to supply them to it, and the effects which may hence result. are not so limited as those which ordinarily attract our attention; but the analysis which they allow us to make is instructive. We observe that the impulse is sometimes absorbed and retained by the grey matter and the systems which it connects, while at other times, on the contrary, it is permitted such unlimited action that it exhausts its stores of force.

Form of the movements.—The ensuing movements may be very different, according to whether the sensory or the corresponding motor root is stimulated. When applied to the motor nerve, the stimulation induces a *simultaneous* contraction of all the muscles to which it is distributed. When applied to the sensory nerve, in passing through the grey matter it undergoes a *rearrangement* which gives a definite direction to the movement; without taking into account that it may be diffused in the area of the neighbouring motor nerves.

6. **General direction of the current of impulse; method of its determination.**—In order to determine the direction in which the impulse is transmitted, in the different nerves and in the systems which they constitute, two methods are available: the one *indirect*, the other *direct*.

The indirect method consists in taking as controls certain phenomena of movement or of sensation of which the situation in the animal experimented upon with regard to the stimulated nerve has been noticed.

The direct method consists in collecting, from the nerves themselves, indices of their activity in the different points of the course supposed to be traversed by the impulse, by verifying their negative variation or current of action. It is true that it is necessary to mutilate the nerve at the very point where it is desired to collect its electrical current.

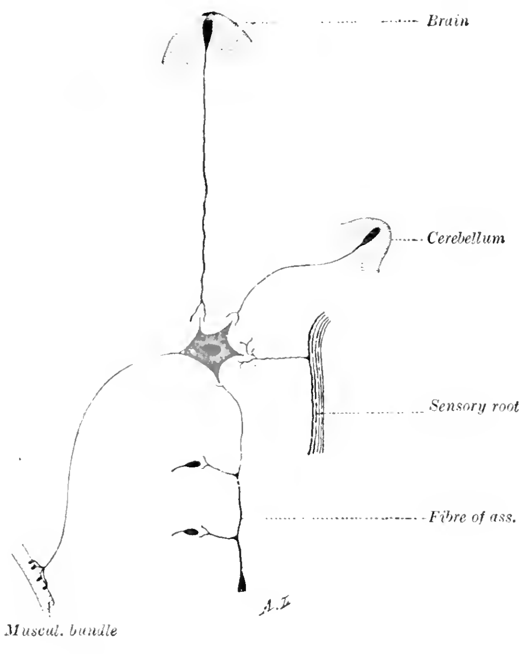


FIG. 104.—Convergence of impulses of different sources on a radicular motor element.

Overlapping of the polar fields.

The information furnished by the two methods is, further, concordant and mutually complete.

Irreversibility of the reflex cycle.—The posterior and anterior roots having

been laid bare, the first are connected with a stimulating apparatus (sledge induction apparatus of du Bois) and the second to a galvanometer. Every time that the central end of the posterior root is stimulated there will be a galvanometric deviation as regards the anterior root. The galvanometer points out, as would the muscle (but in a more direct manner), that the stimulation of the posterior root is transmitted to the anterior root.

Let the arrangement be now reversed, as has been effected by Mislawsky, by connecting the anterior root with the induction coil and the posterior root with the galvanometer. Stimulation of the anterior root will not produce deviation of the galvanometer which is connected with the posterior root. As a matter of fact, however, stimulation travels to the spinal cord. If this root be detached from the spinal cord in order that its central end may be connected with the galvanometer, a deviation at the instant of stimulation will be observed. It is, indeed, on the results of experiments of this kind that the common conductivity of nerve fibres is based. But if the impulse received by a neuron can thus freely traverse it in both directions, this impulse is transmitted from one neuron to another in one direction only, as is shown by the experiment of Mislawsky.

According to the terms ordinarily used, *the impulse proceeds from the terminal or collateral ramification to the dendrites of other neurons* (when these neurons are connected amongst themselves), *and not conversely.* It may also be said : *it proceeds from an emissive to a receptive pole, but never from a receptive to an emissive pole.* There is here manifestly an arrangement, the nature of which is unknown, which hinders the impulse from going backwards from the second to the first, and which determines the direction of the currents of stimulation through the nervous system. It may be compared to the valves of the circulatory system which, situated in the heart, imprint on the movement of the blood a definite direction, while this movement is free as regards its direction in all the rest of the system.

Other examples.—If a posterior root be stimulated and a derivation of the currents of action of the spinal cord be received (after section of the cord below the medulla oblongata), a deviation is observed. If an anterior root be stimulated, there is no deviation. If the spinal cord be stimulated and the currents in the anterior root be received, there is deviation.

All these facts agree with the former experiments of Magendie, which, by the motor and sensory effects of stimulation of the roots, have shown the general direction of the propagation of this excitation. The new fact which has been established is the localization of the directive force in the grey matter, and more precisely, at the point of union of the poles of opposite denominations of the neurons. It should be observed that this directive condition, which is an important function of the *nerve centres*, is not localized in the nerve cells.

Directing organ.—The nerve cells are generally situated in the immediate neighbourhood of the polar arborizations of the neurons ; whence it follows that, in considering only the abortive indications of experiment, the rôle of organs directive of excitation may be attributed to them as well as to these arborizations themselves. It is thus in the ganglia of the great sympathetic, as well as in the spinal cord and brain ; and this has given rise to the idea that the nerve cells are the true centres in the sense which is attached to the word. There are, however, neurons whose original cells are situated at a great distance from their polar extremities. These are the nerves of cutaneous sensation, which pass, as is well known, through the spinal ganglia situated on the posterior roots. If the spinal cell is a reflex centre, it should behave as does every other reflex centre, that is to say, should permit the impulse to pass only in one direction, from the skin to the spinal cord, and not conversely. But no experiment is known which proves that this is the case, and it is on the contrary admitted without contradic-

tion that the impulse may pass from the post-ganglionic segment to the pre-ganglionic segment of the sensory nerve. Another experiment, performed by Langley, is equally significant. When certain ganglia of the great sympathetic are subjected to the action of nicotine, the pre-ganglionic segment becomes inexcitable, while the post-ganglionic preserves its excitability ; in other words, when nicotine is brought in contact with a ganglion of the great sympathetic it prevents the impulse from passing through it. If this experiment be repeated on a spinal ganglion, the result is no longer the same ; the two segments, pre- and post-ganglionic, remain excitable. Thus the physiological reagent employed, nicotine, meets in the ganglia of the great sympathetic with a condition of activity which it does not experience in the spinal ganglia. As nerve cells exist in both, this condition is not due to the cell ; as polar connexions exist in the first and not in the second (at least, so far as concerns the transmission of cutaneous impressions to the spinal cord), it is reasonable to assume that these polar connexions are the organ on which the reagent employed acts.

7. **Dispersion of the excitation ; its laws.**—The stimulation of a sensory region, or of a sensory nerve, is reflected in the grey matter of the spinal cord, in order to return to the muscles, through the motor nerve. According to the intensity of the stimulation, the resulting movements will be *localized* or more or less *generalized*. The dispersion of the excitation follows certain laws which have been formulated by Pflüger, whose name they bear, but which are based on the results separately ascertained or recognized by a number of earlier authors (Herbert-Mayo, Calmeil, etc., etc.) : (1) *If the movements are unilateral, they take place on the same side as the sensory nerve stimulated ;* (2) *If the movements are bilateral, they occur in symmetrical muscles ;* (3) *Bilateral movements following a unilateral stimulation are of the same form, but stronger on the side of stimulation ;* (4) *The transmission of the impulse, when it is generalized, may be performed just as well from the cephalic extremity to the caudal extremity as inversely.* This fourth law has taken the place of another incorrectly formulated, according to which the propagation of the impulse can only be effected from the cephalic extremity.

According to these facts, the impulse, in extending over the nervous system, would appear to invade first of all the nearest regions, and then those more remote : as if it were necessary for it to overcome a certain resistance which tends to limit its extension, and it traverses a longer or shorter route according to its initial intensity or the state of excitability of the grey matter. This is the simple law of its propagation and of its dispersion verified on an apparatus, the organization of which is itself relatively simple, viz., the spinal cord separated from the medulla oblongata : but it must not be forgotten that *the exercise of function creates routes of less resistance, by which the most remote organs may themselves transmit the impulse,* to the exclusion of other routes situated nearer. Applicable to cutaneous or artificial

excitation of sensory nerves, the preceding laws would no longer apply as regards the detail of functions.

If the medulla oblongata is alone preserved, it is in it that the impulses tend to become concentrated, and it is it on which the duty is imposed of rearranging and distributing them. Should the brain take part in the process, every trace of the preceding simplicity disappears.

Numerous exceptions.—Even in operating on the separated spinal cord, the laws of Pflüger are subject to numerous exceptions, as has been remarked by many observers, and particularly by Sherrington, who has made a special study of the question. These so-called laws can only be regarded as schemes which must be adjusted to each individual case. It is easily understood, indeed, that special functions, such as walking, vision, etc. which involve combinations of movements, some alternative, others simultaneous, some symmetrical, others unsymmetrical, cannot be compressed into such simple formulæ. These formulæ express a tendency, but nothing more.

7. **Classification of reflexes.**—Longet has gathered together a certain number of reflex acts which he has arranged in categories, by taking as a foundation the starting-point of the excitation and the point in which the motor reaction terminates. Two nerve systems are usually distinguished, corresponding to two orders of functions and of organs : the one concerned with nutritive acts, the other with external relations. The examples collected by Longet show that each of these systems contains intrinsic reflex cycles ; but, further, that each one is connected with the other : sensory nerves of the one with motor nerves of the other, and conversely.

Let N represent nutrition, R external relations, and let the direction of the propagation of the impulse be indicated by an arrow. There are four possible complications : NN, RR, NR, RN. The best known examples may be arranged in the form of a table. These examples

Elements of the Cycle.	Sensory Excitations.	Motor Reactions.
$N \rightarrow N$	Arrival of the aliments in the digestive tube.	Movements of the œsophagus, of the stomach and the intestine.
$R \rightarrow R$	Abrupt movement menacing the eye.	Blinking of the eyelids.
$N \rightarrow R$	Presence of worms irritating the intestine.	Convulsions of the limbs.
$R \rightarrow N$	Painful excitations of the skin.	Generalized vascular constriction.

could be multiplied to infinity. It would be easy to make numerous divisions and subdivisions for each one of these categories, corresponding to different orders of sensation and of motor reaction. The number of combinations would increase in such a way as to defy every description and schematic representation. It is easier to say that *every sensory element can be brought into reflex relation with every motor element*, for the exercise of the multiple functions, whether of detail or of the whole, by which life is maintained.

9. **Reflex centres of the spinal cord.**—Reflex centres are found wherever the grey matter occurs. The spinal cord contains them throughout its length. Physiology proves this by showing that, after isolation of each of the metameric segments of this organ, the impulse finds a way across it, in order to proceed from the posterior to the anterior root. Anatomy confirms this fact, by showing that the terminal arborizations of the neurons of the first come in contact with the initial arborizations of those of the second.

Principal medullary centre ; Goll's Nucleus.—Physiology also has long demonstrated (even in the dog and in the frog) one or more reflex centres more important than the rest, situated in the superior portion of the spinal cord, and indeed encroaching on the medulla oblongata. Experiments performed long ago have shown what an advantage it is for sensory impulses to pass through these elevated regions in order to reach the nerves of organic life (pupillary nerves, vaso-motors) with certainty and efficiency. The somewhat more recent experiments of Rosenthal and Mendelsohn have shown that it is the same as regards those which reach the motor nerves of the limbs (nerves of the so-called life of relation) ; they do not exert all their effects, from the reflex point of view, except by passing through the nucleus of Goll situated in the superior portion of the spinal cord, and here, also, anatomy confirms the physiological fact by enabling us to follow the intramedullary prolongations of the posterior roots, whose ascending branches (giving off the already mentioned collaterals on their course) ascend to Goll's nucleus in order to seek those paths which bring back the impulse to the organs of the motor nerves. There is here an important reflex centre.

10. **Encephalic, subcortical centres.**—The opto-striate bodies are also centres of this nature of a higher function and more completely organized, but still reflex, presiding over instinctive movements intermediate between reflex automatism and the contingent demeanour of the voluntary movements.

11. **Reflex cortical centres.**—The cerebral cortex acts as a reflex centre under many different circumstances. The acts (of involuntary

nature) of the deeply seated organs have in it their automatic regulative centres. The most complicated acts of the life of relation can take place, like the preceding, in an automatic fashion, without direct participation of individual consciousness and will.

The condition of the reflexes in pathology.—It has long been observed clinically that, in cases of more or less total interruption of the conducting fibres of the spinal cord, reflex movements exist in the inferior limb, and indeed are often increased. These clinical facts are satisfactorily explained by the definite results of physiological experiments. But in looking at them more closely, it is necessary to allow that the conditions on both sides are not so identical as was formerly supposed to be the case.

Medullary reflexes.—Of the old conclusions which had been admitted without question, this one still remains: these reflex movements, those which are normal as well as those provoked by excitations of the sensory localities or sensory nerves, may be observed, even in man, after complete interruption of the spinal cord. They are also observed in the ape after experimental section of the cord. But instead of being very quickly recovered, as in the dog and the frog, and of becoming exaggerated as in these animals, they may remain in abeyance during days or weeks, only reappearing slowly and remaining feeble.

Cerebral reflexes.—The movements known as reflex, on account of their automatic occurrence, are not the exclusive attribute of the spinal cord, and of its bulbar prolongation, while voluntary movements would only appertain to the brain, as has been long believed. *All the areas of the grey matter, wherever found, including the cerebral cortex, are capable of automatically reflecting impulses;* this is the primary function of the grey matter. To this function, the simplest which effects movements adapted to a general end and following a simple general law, is superadded another, which is in reality nothing but its perfected expression, that of producing varied movements according to contingent indications, movements which are described as voluntary. This function is not the attribute of grey matter of a particular kind, and in consequence privileged, but depends upon a more complete union of the nerve groups amongst themselves. The privilege of the grey matter of the cortex consists in the number and the power of its associations, which ensure the exercise of that which is known as intelligence and will. Should these associations be resolved into their elementary component systems, the brain will then operate as a reflex or automatic organ. Not only is the brain not deprived of a reflex function, but the cerebral reflexes are the most numerous of all, on account of the large number of elementary systems which enter into its constitution.

Post-hemiplegic contraction.—It is often, but not invariably observed, that in hemiplegic patients an augmentation of the muscular tone of the paralysed limbs occurs, which must be regarded as an instance of a reflex phenomenon (tonic reflex and no longer clonic reflex). Its explanation is less simple than that of the preceding facts. Indeed, it differs from them especially in this, that the total interruption of the spinal cord is not only not a determining condition, but renders impossible the onset of the phenomenon. Many explanations of this phenomenon have been proposed, of which each is based on some hypothesis concerning the function of the conducting fibres which unite the grey masses or superior surfaces to the grey columns of the spinal cord; all agree in this, that there is, from the fact of the lesion which has produced hemiplegia, a loss of some antagonistic force which, being no longer counterbalanced, leaves the field free to reflex motor action. By some, this antagonism is regarded as purely motor and as being exercised between the muscular forces spared by the para-

lysis, for the benefit of those whose centres have been the best preserved. It has affected, for example, the extensors and the flexors unequally, the first being more seriously involved than the second ; in this case the member contracts. By others, the antagonism is looked upon as existing between the two nerve forces, the one of stimulation the other of inhibition, which are more and more firmly believed to co-exist in the nervous system, represented as they are by fibres which are individually distinct, although often mingled in the tracts. From the brain an inhibitory influence would descend into the spinal cord by way of the pyramidal tracts. Degeneration of the latter, by suppressing this influence, would leave the field free to motor impulses, and would in this way result in contraction. But, as regards the site at which these impulses are reflected, some would place it in the spinal cord, as in the old theory of the reflex (P. Marie). For these the necessary and sufficient condition of the contraction is the interruption of the pyramidal tracts. Others would look upon these impulses as ascending to the brain, whence they would redescend by special paths, the cerebro-ponto-cerebellar tracts, in order to reach the spinal cord. For these latter a necessary condition of the contraction would be not only the destruction of the pyramidal tract, but also the conservation of the cerebro-ponto-cerebellar tracts.

B. SUSPENSION OF THE EXCITATIONS ; ACTION OF ARREST OR INHIBITION

In the reflex act, the excitation of an element is communicated to one or several other elements which follow it. *In the inhibitory act, the effect of an excitation is to suspend, or to render momentarily impossible, this transmission of the impulse from one element to one or several other elements.*

1. **Its scheme.**—The reflex scheme presupposes at least two neurons, indeed two groups of neurons, connected in succession.

The scheme of inhibition, such as it may be represented according to the known facts which have served to prove its existence, presupposes at least three of these ; two of them being arranged end to end, in order to form the fundamental reflex arc ; towards their point of association a third converges, the function of which is to hinder the transmission of the impulse from the first to the second. It is unnecessary to add that these are purely imaginary representations, and that in reality we deal with complex nerve masses, which we endeavour to reduce to their most simple type, but without ever being sure of succeeding in doing so.

Its seat.—The locality in which this inhibitory phenomenon takes place is, once again, the grey matter wherever it occurs (great sympathetic ganglion, grey axis of the spinal cord and of the medulla oblongata, ganglia and cortex of the brain, etc.). And amongst the alterations that this substance impresses on the progress of impulses, this is not one of the least remarkable. At the same time as the seat of the phenomenon, it is necessary to define the sense of the word ; it is important to ascertain with exactitude the conditions which must

be fulfilled in order that it may occur and which enable it to be distinguished from other apparently similar phenomena.

Apparently paradoxical datum.—Inhibition, nerve arrest, is not a fact whose existence necessarily occurs to the mind. On the contrary, at the first glance this fact appears to be paradoxical, and it is experiment which enables us to realize it. It is accepted as an axiom that all muscular activity implies (in the normal performance of function in the organism) a nervous activity which presides over it. And further, it has been accepted for a long time, as a necessary consequence of this fact, that muscular repose implies repose of the nervous system. But experiment has shown (and this is the very essence of the inhibitory phenomenon) *that muscular repose may be the consequence of nerve activity.* In other words, the excitation of certain nerves may be rendered evident by the activity of the muscles with which they are in mediate or immediate relationship; but, further, the excitation of certain other nerves may be made manifest by the stoppage or the non-execution of the movement of the muscles with which they have certain relations, regarded as mediate. An example is necessary to support this distinction.

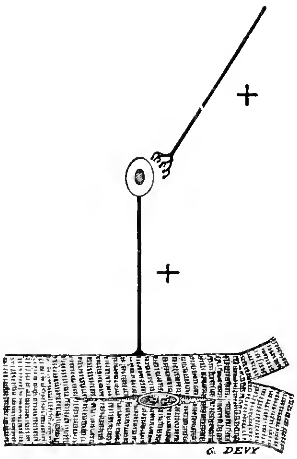


FIG. 105.—Diagram of the antagonistic action of the excito-motor and inhibitory nerves on the terminal nerves.

This action is exerted by the connexions of these different elements between themselves in the grey matter of the ganglia or motor nuclei.

Example.—The heart receives from the spinal cord, through the great sympathetic, nerves whose stimulation is rendered evident by exaggeration of its movements (beating or cardiac systole); it receives others from the medulla oblongata by way of the pneumogastric, whose excitation is followed by the slowing or temporary stoppage of its movements. These nerves supplied the first known example of nerve arrest. The fact was observed by the brothers Weber (1845) and was afterwards confirmed by numerous observers; not, it is true, without a prolonged discussion concerning its exact signification.

Numerous meanings attached to the word inhibition.—Whenever a new phenomenon takes its place in a science, a new and special term is necessary in order to designate it. Suspension of the activity of an organ by the arousing of activity in a nerve supplying it, was first called "stoppage." Later, Brown-Séquard proposed the term "inhibition," of which the great success is well known. Brown-Séquard made no attempt to narrowly define the characters of the pheno-

menon, but, under the name of inhibition, he, on the contrary, gathered together all the facts which had a near or remote analogy with it.

Instead of a clearly defined signification, the new word assumed a metaphorical and indeterminate meaning.

Inhibition and paralysis.—However, in his definition of inhibition, the preceding author still maintained (at least, theoretically, if he did not succeed in justifying it by the examples he brought forward) the idea of the contrast existing between the exciting nature of the cause and the depressive aspect of the result. It may be said, indeed, that he exaggerated it, by seeing, in every loss of function, the effect, not of a destruction, but of a stimulation. But for some years this particular meaning has been steadily losing ground. It is possible to read in a number of works that curare inhibits motor nerves, that chloroform inhibits sensation, etc.[1] To designate these toxic phenomena and other similar ones which involve a loss of function, a word has for long been available, and a very definite one, namely *paralysis*, and this is the only one which is appropriate. By closely assimilating inhibition and paralysis, the very idea which this new word (inhibition) was intended to indicate disappears. In order to prevent this confusion, it is necessary to return to the experimental datum which lies at the foundation of the conception of inhibition. *This appellation will be given to every phenomenon reproducing the characters and the essential conditions of stoppage of the heart by the stimulation of the vagus nerves.* Among the numerous phenomena to which the name of inhibition has been given there is a certain number which has some analogy to the stoppage of the heart, along with many others which have no connexion with it. It is necessary to be aware that the classification of the facts from this point of view is often uncertain and difficult to effect. While waiting until this classification may be rendered exact, it is desirable to be careful in the employment of the word.

FIG. 106.—Stoppage of the heart by stimulation of the vagus in the turtle (laboratory tracing).

Latent period of some duration. Post-compensatory exaggeration of the systoles after stoppage.

It is necessary also to be aware that, in current literature, it includes phenomena, doubtless analogous, but which nevertheless differ greatly the one from the other.

Inhibition and shock.—When a shock of a certain violence acts on a tissue (nervous tissue principally), a temporary alteration may occur in it which renders it unable to manifest its activity. This is seen in cerebral *concussion* as well as in spinal or nervous concussion. This inability to react is obviously of the nature of *paralysis* induced by direct loss of function. Hence it is wrongly regarded as an inhibition. In any case the mechanism of the phenomenon, and the appropriateness of its designation, are open to discussion.

But the pathological phenomenon to which the name of *shock* has been given may present different forms, causes and mechanism. As the result of serious wounds involving organs which are remote from the centres, a severe depression of the whole nervous system sometimes ensues ; and it is reasonably explained by an influence, probably irritative, which, emanating from the wound, reaches

[1] The word is even employed by certain chemists, for whom sulphuric acid would inhibit sulphate of soda, and reciprocally.

the nervous centres by the way of the sensory nerves. This case resembles inhibition such as it is defined in physiology (an activity which prevents the manifestation of other activities). In this special case, but not in that in which the nervous organ is directly wounded, it is right to speak of inhibition.

Inhibition and fatigue.—When the nerves of an organ have been stimulated severely and for a long time, the organ becomes for a certain period incapable of functional activity. This functional incapacity is not paralysis, but fatigue. Some observers would not hesitate to describe this phenomenon also as inhibition. This is a new confusion added to the preceding. Paralysis, fatigue, and inhibition resemble one another doubtless, in that they manifest themselves by an inactivity (persistent or temporary) of organs; but on this account the three terms are not synonyms expressing inactivity. Each one of the three has its exact signification; each one indicates an inactivity of a special kind, of a special mechanism. It is as if, the *effect* being fundamentally the same, the *conditions* of its production differ absolutely in the three cases, and the special terms made use of to characterize the three phenomena are meant to point out the conditions on which they depend.

2. **Analysis of the system.**—It is now tolerably easy to show that the scheme of innervation of the heart corresponds, in its main outlines, to that which we have traced above with regard to a system capable of producing inhibition. The heart possesses ganglia which are nothing else than scattered masses of grey nervous matter. From these ganglia short neurons arise, which proceed to the myocardium; these are the motor nerves, properly so called, of the heart. In these ganglia terminate neurons of great length coming, some from the spinal cord, others from the medulla oblongata, which form with the grey matter connexions of such nature that the stimulation of both has, so to say, opposite effects: that of the first is transmitted (not without modification) to the motor elements of the heart; that of the second produces an obstacle to such a transmission, and deprives the myocardium of its habitual source of excitation, whence its temporary stoppage.

Of the three portions which are regarded as necessary, the first suppresses one, and causes the inhibitory nerve with the motor nerve to converge on the muscle, to which each one of the two would convey an inverse, or reciprocally antagonistic, influence; the others suppress two and only admit a single element, alternatively motor or inhibitory, according to circumstances. But facts contradict this manner of viewing the matter.

Distinct existence of inhibitory nerves.—Inhibition (arrest by excitation) necessarily depends on conditions which appertain either to the stimulating agent or to the substance excited. Therefore it does not depend on the conditions of the excitation. It is, in fact, produced by stimuli, which are the very same as those which put the motor nerves in action. It ceases to be produced, on the other hand, with

stimuli which are inefficacious (by default or by excess) when they are made use of on motor nerves. Hence neurons exist whose specific function it is to produce inhibition. It is possible that the same neuron may produce inhibition by one of its terminations and excitation by another, but it is necessary always to admit the existence of a terminal specific and inhibitory apparatus.

Objection.—Some observers (Schiff, Moleschott) have endeavoured to refer inhibition to a phenomenon of ordinary paralysis. They maintain that the stoppage of the heart by stimulation of the vagus arises simply from an alteration of the motor properties of the fibres of this nerve, which are excited in special conditions, and hence deprived of their motor power.

Reply. Different proofs.—The objection falls to the ground through the fact,

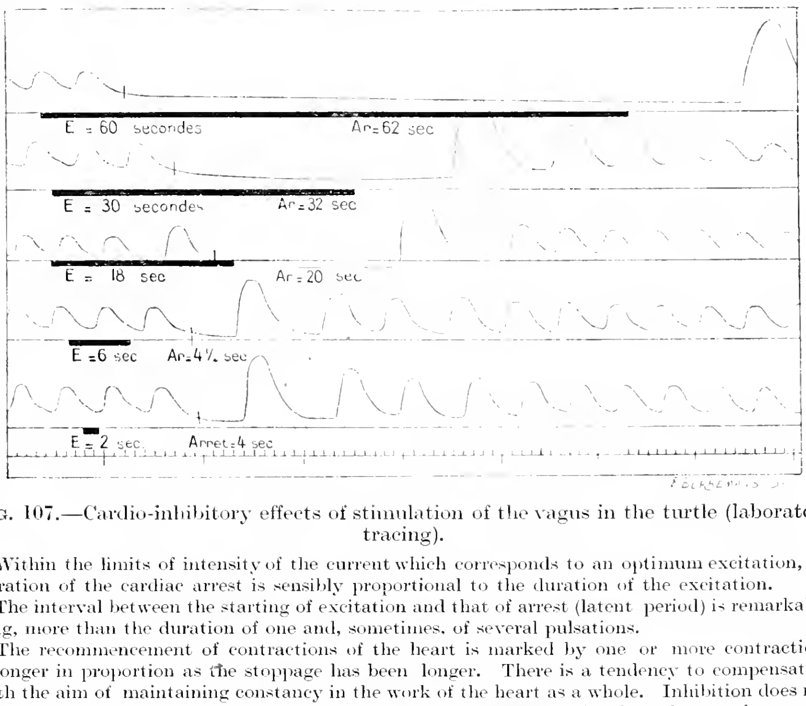


Fig. 107.—Cardio-inhibitory effects of stimulation of the vagus in the turtle (laboratory tracing).

Within the limits of intensity of the current which corresponds to an optimum excitation, the duration of the cardiac arrest is sensibly proportional to the duration of the excitation.

The interval between the starting of excitation and that of arrest (latent period) is remarkably long, more than the duration of one and, sometimes, of several pulsations.

The recommencement of contractions of the heart is marked by one or more contractions stronger in proportion as the stoppage has been longer. There is a tendency to compensation with the aim of maintaining constancy in the work of the heart as a whole. Inhibition does not act by destroying, but by suspending and preserving the stimulation brought to the muscle by its motor nerves.

which may be easily proved, that the stimulus required in order to ensure stoppage by exciting the vagus has the same qualities as that which is required to call into action the accelerator nerves of the heart.

Excitation in parallel series.—A very convincing aspect may be given to this demonstration by making the ordinary conditions of stimulation (intensity, frequency, etc.) vary in a graduated series. In such a case the response of the motor nerve goes through a series of phases characterized by a minimum, an optimum and a pessimum, indicating that the excitation is successively inefficacious by default, then efficacious, and finally once again inefficacious by excess. But this is precisely what is observed with inhibitory nerves, yet with this differ-

ence corresponding to their function, that the response is not movement, but the stoppage of movement (Morat).

Effects of fatigue.—Another proof of the same kind: in the prolonged stimulation of the *motor* nerve, *fatigue* of the apparatus, which ensues after a certain time, *hinders the continuation of the movement.* In prolonged excitation of an *inhibitory* nerve, *fatigue* also occurs, but with this difference, that it *hinders the continuation of the stoppage* and consequently causes the reappearance of movement. Hence the stoppage is indeed in this case a result of the activity of the stimulated nerve, and not a consequence of its alteration; for if activity involves fatigue, alteration, that is to say destruction, does not involve it.

Invariability of the effects of the excitation.—If inhibition was connected with certain variable conditions according to the nature of the nerve, it would be possible to obtain inhibition, in certain cases, by stimulating the accelerators of the heart and, conversely, acceleration by exciting the pneumogastric. But this is not the case. The trunk of the tenth pair contains, it is true, accelerating fibres, the existence of which can be demonstrated, not by modifying the nature of the stimulus, but by paralysing the inhibitory fibres with belladonna; but its origins do not contain any of these fibres, and the invariable result of the stimulation of these origins is slowing or stoppage of the heart (Heidenhain).

Another objection.—By applying the stimulus to the white matter of the brain, sometimes motor effects, sometimes inhibitory effects ensue, yet nevertheless no distinct fasciculation can be discovered in this substance to which inhibition rather than motor activity can be attributed; hence it has been supposed that, as regards this organ at least, the same fibres are, according to circumstances, motor and inhibitory.

Reply.—In the same organ (the brain) the manifestations of sensation and motion are in many points inextricably mixed. But we do not hence conclude that they belong indifferently to the same elements, but to distinct elements which are confused together. And this reasoning holds for inhibition as it holds for the other specific functions which are discharged by the functional activity of the nervous system. It is sufficient that the proof of this functional distinction has been established in certain typical cases in which analysis is possible. The cases which are refractory to analysis ought not to be appealed to as invalidating this proof, or as proving the existence of properties of nerve elements which are incompatible with those conferred from other sources.

Field of inhibition.—The examples of authentic and invariable inhibitory nerves are continually increasing. They exist for the vessels as well as for the heart; for the intestine as well as for the circulatory apparatus.

Inhibition is represented in all the partial systems which make up the nervous system; and it everywhere obeys the same law: it is governed by special nerves in the partial nervous systems.

Specific nature of the relationships.—*The three constituent elements of the system constructed in this way each possesses the fundamental properties of the nervous element* (excitability and conductivity), and so far are not distinguishable the one from the other; *but they have each a specific nature as regards the connexions which they contract at their extremities.* The one enters into relationship with the cardiac muscle like an ordinary nerve, the two others form a relation with the grey ganglionic matter, and these relations, which cannot be defined by anatomy, are clearly different for each of them.

Inhibition is an internal phenomenon of the nervous system.—Hence

inhibition, in order to take place in its habitual and normal conditions, requires the activity of a nerve which has special relationships with other nerves, and without this activity it does not occur. The very curious consequence of this activity of the nerve is the repose of a muscle (or of an analogous organ); but this muscular repose is itself the consequence of the repose imposed on its motor nerve. It is on this account that *inhibition is called an internal phenomenon of the nervous system.* The still unknown mechanism which gives origin to it is perfected in the grey matter wherever the latter exists, because the phenomenon of inhibition is general, and is met with in all functions and in each of their degrees. The inhibitory nerves never pass beyond the most superficial layer of this grey matter; they correspond to what was formerly known as the *intercentral fibres* and to what are now called *elements of association*, elements whose two extremities, initial and terminal, are embedded in nervous grey matter and have no direct contact with organs.

The grey matter in the nervous system presents superposed layers; hence it has a superior and inferior limit. As regards the muscles of the skeleton, this inferior limit is in the grey medullary axis; as regards the muscles and other visceral organs, it is in the ganglia of the chain of the great sympathetic. If our scheme of inhibition is exact, there should not be in the nerve trunks which proceed from the spinal cord to the muscles of the skeleton any inhibitory element. Experiment verifies this induction; by stimulating an extra-medullary motor nerve of a skeletal muscle, nothing but its contraction has been realized, stoppage of its movement has never occurred. But these inhibitory fibres are met with in the cerebral and spinal tracts. They are, in truth, difficult to demonstrate by stimulation, because they are mixed with the fibres which give rise to movement, and there is no means of separately irritating them; but, nevertheless, their existence has been proved.

The great sympathetic (to which the pneumogastric is united by the majority of its elements) affords, on the other hand, on account of the dissemination of its branches through other tissues, an exceptionally easy means for the separate stimulation of its tracts of different function: this is doubtless the reason why the phenomena of stoppage have been recognized in it before being suspected in the remainder of the nervous system. On the other hand, the motor neurons which proceed from its ganglia to the organs of visceral movement are often embedded in the tissue of the latter, and run so short a course that inhibition appears to be effected in these very organs themselves: this is precisely what occurs in the heart. It may neverthless be shown that the grey matter of the ganglia is a locality in which the inhibitory elements of the great sympathetic terminate.

Experiment.—In a rabbit the chain of the great sympathetic is exposed, in

front and behind the ganglia of the base of the neck ; an excitation made posteriorly, that is to say, above these ganglia, inhibits the vascular muscles of the external ear, which is rendered evident by an intense vaso-dilatation of this organ (Dastre and Morat). Excitation applied anteriorly, that is to say, below these ganglia, contracts these vascular muscles, as is proved by the pallor of the same organ. The site of the inhibition is clearly in the ganglia, which thus indicates the starting point from which this inversion of effects occurs.

3. **Excitation and inhibition.**—In short, the inhibitory neuron receives normally by its dendrites, or artificially during its course, a stimulus which has no need of any special quality in order to cause it to fulfil its function. This stimulus traverses the neuron and proceeds to terminal arborizations. When it has arrived at its destination it produces that special effect which is rendered evident by the repose, the non-activity of the motor neuron to which it is distributed. This effect in different intensities is invariably the same as regards the neuro-motor apparatus thus brought into relationship with the excited elements. But the terminal connexions of the inhibitory neuron are multiple. While certain of them are in inhibitory relationship with given neuro-muscular elements, others may be in relationship of excitation with other elements, in such a manner that stimulation has a double effect, partly inhibitory, partly motor, no longer successive but simultaneous, and it is in this sense only that it can be said that the same fibre is both motor and inhibitory. This double relation has a definite object : when, for example, two muscles are antagonistic one to the other, and when a movement should ensue in one of them, there is an economy of force if, by the aid of the nervous system, the one can be relaxed while the other contracts.

Thanks to the multiplicity and the variety of its terminal polar connexions, *one and the same fibre may be excito-motor in function for certain* of the elements with which it enters into relationship, *and inhibitory for certain* other of these elements. But experiment shows that *these relationships are not capable of being inverted.*

Reflex action and inhibition combined in the same Cycle.—The reflex action and the inhibitory action may thus co-exist *simultaneously* in a mass of grey matter ; they represent as a whole but one aspect of the numerous functions of this matter. On the other hand, these two actions are also associated in *succession ;* for example, a stimulation of the skin is transmitted to the spinal cord by its sensory nerves, is thence reflected to an inhibitory nerve, such as the vagus, by it conveyed to the ganglia of the heart and causes stoppage of this organ : this is one of the ways in which cardiac syncope is brought about. Again, this stimulus may be reflected in the form of an inhibition to some gland whose secretion it stops, as Gley has observed for the sub-

maxillary gland. Yet again, it may be reflected so as to exert an inhibitory influence on some muscle of the skeleton whose commencing contraction it arrests, as Beaunis has observed. In all these examples it passes through a chain of neurons, in the course of which at one of the halting places it changes its character, that is to say, from being a promoter of contraction it becomes an obstacle to the same. It is not always easy to clearly ascertain the situation of this remarkable halting-place. One thing is certain, however, that it is neither wholly at the commencement nor wholly at the end of the cycle, but somewhere in its course, in what is called the centres of the nervous system.

The impulse, which starts from a limited sensory area (for instance, from a portion of the cutaneous surface), in order to proceed to an equally defined motor organ (for instance, the heart), passes through a system of neurons which are at first *divergent* and afterwards *convergent*, impressing on it numerous and distinct modifications, some *parallel* others *successive*. The direction of the reactional effect expresses the *resultant* of the numerous conflicts which take place in this aggregate. It is the intrinsic complexity of this system which renders it able to react in a varied manner as regards stimuli which seem to be identical. It is certain that it is not at times consistent with itself. It is this *complexus of neurons* which many, for simplicity's sake, have endeavoured to reduce to a single element, possessing now the "motor property," now the "inhibitory property." The attempt is praiseworthy, but it is opposed to the facts both of anatomy and of experiment.

Inhibition, dynamogeny.—The study of the nervous system leads us to suspect in it the existence, not only of functions which are clearly defined, such as reflex action and inhibition, but also of others which are more obscure, the necessity of which we understand without being able to ascertain their determination. Stimulations of a sensory nerve often produces very diverse effects in the grey matter which receives the stimulus. Sometimes it suppresses certain of the communications which exist between the elements of the latter and diminishes the motor effects over which this grey matter presides: this result is due to inhibition. Sometimes, on the contrary, these communications seem to be reinforced and extended, and the flow of impulses increases as it passes through the grey matter: this is the phenomenon to which Brown-Séquard gave the name of *dynamogeny*. According to these facts, we learn that the grey matter possesses a directive function, or one of orientation, no longer general like that determining the total current, which causes the impulses to move forward in proceeding from the sensory organs to those executive of functions, but a particular, localized and contingent function, which in the complicated network formed by the nervous paths makes them take such and such a branch road rather than any other. This is the function which, in the German language, Exner has described by the word "*Bahnung*," for which it would be difficult to find a suitable equivalent: but if the creation of a word be permissible, perhaps the expression "viatility" may serve to indicate the idea of the facilitation of transmission brought about by this function.

4. **Mechanism of inhibition.**—This is totally unknown to us, as is also that of reflex action. This latter is, however, more easy of comprehension in the sense that it demonstrates to us the communication of the movement of one body to another; while in inhibition it is the

movement of a body which is made use of to render another body immobile. Doubtless physical science, both molar and molecular, furnishes examples of effects of this nature; but, so long as we are unable to precisely define the nature of the movement which is thus produced and arrested, every theoretical attempt at explanation will have merely the value of a comparison. These comparisons show us that the phenomenon may be included in the category of explicable facts, but the explanation itself is wanting.

5. **Secondary effects of inhibitory excitation.**—The stoppage of the movement of organs is the most striking fact of inhibitory activity, but it is not the only one. The following fact must be taken into consideration. If the movements of the heart are recorded and the vagus stimulated, the tracing indicates suspension of its beats; then these latter recur after the excitation; but this remarkable fact is observed that, during this recurrence of the beats, they are at first stronger or more numerous; to such an extent, indeed, that if the work of the heart be calculated before and after the stimulation (for equal periods of time), the two amounts are practically equal. The same observation can be made conversely when the motor nerves of the heart are stimulated in order to accelerate its action. The acceleration which ensues is followed by a compensatory retardation (Marey).

As regards regular functions, such as that of the heart, nerve stimulation, whether it be provocative or inhibitory, would not then cause a change in the total quantity of movement, but would only distribute it in a different manner as regards time.

It may be asked if, as regards space, the stimulus which seems to disappear and to be annihilated in the grey matter, does not merely undergo a change of direction for a certain period.

Inhibition and anabolism.—By *catabolism* is understood the expenditure of energy of the tissues (chiefly of the muscular) during their activity; by *anabolism* is implied the reconstitution of potential which follows this activity: *metabolism* is the aggregation of these operations. The catabolism of the tissues is under the dependence of the nervous system, in the sense that the tissues do not become active unless this system intervenes in order to upset the unstable equilibrium in which they are found in the so-called state of repose. For the sake of uniformity, it has been thought that anabolism should be equally under the dependence of the nervous system. Two kinds of nerves are distributed to the organs: some, strictly motor, are catabolic (provoking expenditure); the others, inhibitory, should be anabolic nerves (working for reconstitution). This conception is seductive, but if examined more closely, it will be obvious that it is in no sense justified. Let us take a particular example, that of the heart, and let us see how its nerves, the activity of which differs, influence its energetic processes.

(a) **Inhibition and heat.**—If the inhibitory nerve of the heart be stimulated, the temperature of this organ falls. It again rises when its movements recom-

mence. Must it therefore be concluded that, during stimulation of the vagus and the repose which results, the heart absorbs heat, which it afterwards gives out ? Certainly not ; the explanation of the phenomenon is far more simple. The stimulation of the vagus, by depriving the heart of the impulses which it normally receives, causes it to economize its combustible reserves, restricts its expenditure of energy, whence the relative lowering of its temperature. There is a diminution of the pre-existing energetic phenomenon ; there is no inversion of this phenomenon.

(b) **Inhibition and the electric current.**—The heart (when it is incised) presents, like other muscles, a current of repose. At the moment of its contraction, this current of repose undergoes a negative variation. If the vagus is then excited, a *positive* variation of this current of repose is observed (Gaskell). How is this phenomenon to be interpreted ? Is it the indication of a reversal of the energetic phenomena, which from being analytic would in the heart become synthetic ? This is certainly not the case.

Here again the explanation is much simpler. A muscle in a state of tonic contraction furnishes a current of repose, which is diminished by the negative variation corresponding to its tonic activity. If we diminish this tone, by inhibiting the muscle, the current of repose will increase ; hence the apparently positive variation of the current ot repose. If we increase this tone by stimulation of the motor nerves, then the negative variation, such as is ordinarily observed, will be produced. In every case, when the polarities are reversed in a circuit it must not be concluded, simply from this fact, that the chemical phenomena which are the cause of it have changed their denomination ; only one thing is certain, namely, that the current has changed its direction.

Asymmetry of the anabolic and catabolic phases.—The belief that the positive variation of the current is connected with muscular anabolism, while its negative variation is connected with its catabolism, corresponds to the other conception that these two processes, the one destructive, the other restorative as regards the muscular reserves, are at the same time symmetrical and opposed, each one of the two phases representing the exactly contrary operation of the preceding. But here again, if the facts are more closely examined, it will be seen that they in no sense justify this manner of regarding the question.

The only tolerably accurate information which we possess concerning muscular metabolism is derived from the study of exchanges with the blood. We see that the blood furnishes glucose and oxygen to the muscle, while the muscle supplies the blood with carbonic acid. Limited though it may be, yet this information has great value concerning the nature of energy. The substance (glucose) which passes from the blood to the muscle (during the anabolic phase) possesses a large amount of energy ; while that (carbonic acid) which is delivered to the muscle from the blood during the catabolic phase is almost totally deprived of energy. This proves that, from the energetic point of view, the anabolic phase, strictly speaking, does not practically exist either in muscles or in any of the animal organs, but rather in the vegetable, which by its chemical syntheses accumulates that provision of energy which it will deliver up to the animal. A proof that this anabolism is of such a nature as to dispense with the nervous system, while catabolism, so active in the animal as compared with the vegetable, is, on the contrary, under the dependence of this system.

Comparison of inhibition with neuro-motor paralysis.—Whether it is a question of the muscular exchanges, of its mechanical work, or of its heat given off, or of its electrical phenomena, we cannot fail to be struck by the following fact : the intervention of the inhibitory nerve acts in the same way as if section of the motor nerve of the muscle in question had been performed. It suppresses in the muscle the impulses which it received from the centres ; it seems, indeed,

that it does still more, and affects it throughout its extent with a momentary incapacity to react, placing it indeed in a state of inactivity which we know to be only transitory, but which is equivalent, so long as it lasts, to paralysis; whence the name of *paralysing nerves* which was formerly given to the inhibitory nerves or to those of arrest.

The paralysis, of which it is here a question (if our comparison is exact), is not then a muscular paralysis, but a paralysis of the motor nerve. *It is by affecting the motor nerve, and not the muscle which follows it, that the inhibitory nerve effects,* at the least expense and temporarily, *that special paralysis which corresponds to inhibition* and which is characterized by the fact that it depends on the activity of a special nerve, the inhibitory nerve.

Lengthening of the muscle.—Whether we either interrupt the anatomical continuity of the motor nerve, or whether we suspend its tonic activity by inhibition, the result in both cases will be the lengthening, not, indeed, active but passive, of its muscles, which thus yield to the exertions of the antagonistic powers. This is what happens in the vascular apparatus both through section of the vaso-constrictors and excitation of the vaso-dilators. De Varigny has observed in the invertebrata, by operating on a muscle of the *Stycopus regalis*, that stimulation sometimes causes very obvious lengthening of this muscle. The explanation of this lengthening probably lies in an inhibitory phenomenon of this nature.

Neuro-muscular paralysis and anabolism.—Let us continue our comparison. Let a muscle be taken of which we have cut the motor nerve between the spinal cord and itself. We will not choose the heart, because this muscle carries with it its portion of the spinal cord, I mean its ganglia, and many other muscles of organic life resemble it in this respect; but the skeletal muscles are available for this experiment of enervation. During the time which immediately follows section of the motor nerve, that is to say, before degenerative processes have commenced in the nerve and muscle, the paralysis of these two organs is purely functional. Both cease to receive the stimuli which are normally sent to them by the nervous centres; they are in a condition of enforced repose. The catabolism which depends on these stimuli ceases in them on this account, or, at all events, is very much reduced; the exchanges are diminished, as also the disengagement of heat; the mechanical work is *nil*; but anabolism persists in this enervated muscle, just as in normal muscle. If a proof of this is sought, it is only necessary to excite its nerve artificially; the muscle will then supply, even to exhaustion, a new amount of energy in the form of work and of heat. In order that it may recuperate, it will suffice to leave it in repose for a certain time. Then, once again, the stimulus may be applied, and so on. If the muscle has remained in connexion with its vessels, matters will take place as just described. If the muscle is detached from the animal, the exhaustion at the end of a certain time will be definite, because then the muscular element works on a provision which is no longer renewable.

Reciprocal bond of union between anabolism and catabolism.—The catabolism of the tissues is directly dependent upon the nervous system; anabolism is not directly dependent upon it: this is clearly obvious from the preceding experiments. There are, nevertheless, between anabolism and catabolism reciprocal bonds of union which ordinary observations render evident. When an organ is entirely and definitively deprived of stimuli, far from anabolism being maintained at its highest level, the organ, on the contrary, atrophies for want of exercise. It is true that, if this organ is excessively stimulated, it may also be compromised by this over-activity. The condition which must be fulfilled is that it receives stimuli in sufficient quantity, without excess and without default. Life is an equilibrium, but this equilibrium is not static, it is, on the

contrary, mobile ; it is based on a current account, of which the receipts and expenses regularly balance ; the irregularity of this account, however induced, is a cause of destruction for the living organization. The nervous system intervenes every moment to hinder it from ceasing or from exaggerating its rapidity. As this current in the animal organism may be compared to a waterfall, it hence follows that every effort of the nervous system is limited to opening the flood-gates when the current is slow,—this is excitation ; and to closing them when it runs too fast, this is inhibition.

C. CONSERVATION OF THE STIMULUS. NERVOUS CIRCULATION

It is clearly obvious that the impulses are preserved in the nervous system ; we see them, indeed, ceaselessly streaming in upon us by the paths of the senses without muscular movement immediately following ; and, on the other hand, this movement may arise in us without external provocation, that is to say, long after the provocation has taken place. *There is a bond of union in time between present motor action and past sensory excitations.* How can this bond of union be explained ? How is it possible to comprehend that the impulse which had no immediate effect, and which seemed to be lost and destroyed in the nervous paths, can, nevertheless, at a given moment reappear with its primitive intensity ? How is this hiatus filled up ?

1. **Circulation of the excitation.**—The condition of excitation, with the consequences which it induces in the nervous system (conscious or unconscious sensation, voluntary or involuntary movement), is governed by an internal movement which is propagated along the nerves at a definite rate. In spite of the retardations or temporary stoppages which it experiences, this molecular movement, which follows a definite direction, will discharge itself in the muscular tissue, if there is no special arrangement by which it can be retained in the nervous system. Excitation, such as we conceive it from the analytical study of the nerve elements, does not imply a stationary condition. Hardly entered into a cycle, the impulse traverses it throughout its length, as the reflex act clearly proves. Arrived at its termination, it has but one means of remaining in it, namely, to reappear by a device, by penetrating once again into its original paths. In a word, *it is only preserved because it circulates in this cycle, and inasmuch as it circulates in it.* How is this circulation carried out, and what are the anatomical conditions which render it possible ?

2. **Automatic excitation.**—In numerous cases the reflex act shows us how this automatic and in some measure indefinite renewal of the excitation is effected. In the mental conception of this act there occurs the predominant idea of a strict dependence of movement upon sensation (conscious or unconscious) ; but this idea expresses only a portion of the truth. This dependence is reciprocal, in the sense that,

if muscular movement in it depends on a sensory excitation, this latter in its turn depends on muscular movement; this is at least what is easily seen in a large number of functional actions of a simple and regular order, such as those which maintain the so-called functions of nutrition (movement of blood in the vessels, or of air in the lungs, etc.).

If this reciprocity, this automatism, escapes us at the first glance, it is because, in endeavouring to make an analysis we have broken it in order to have a clearer conception of the internal or *central* bond which connects movement and sensation. In our own experiments we ourselves furnish the sensory excitation, in order to be sure of its provision, and we receive the muscular movement in a myographic apparatus the better to observe and study it. But this system, open to the exterior, is, we repeat, artificial; in any case, as regards things as they are, it is far from being the rule. An external tie, *peripheral*, thus connects, in its turn, sensation to movement and makes it to depend upon it. The cyclic system, once primed, continues to act functionally by itself. Its losses through excitation are minute, its expenditure of energy is extremely feeble and is compensated by the exchanges effected with the blood circulating in its vessels.

Superposed reflex arcs.—The nervous system is formed of two tiers or two superposed systems, which, placed one above the other, repeat the same more or less complicated scheme; that, namely, of an arc with two branches, representing a double canalization, permeable in the opposite direction to the impulses.

(a) *Inferior Arc.*—The inferior system is formed by the roots of the nervous system; these are elements which branch out from the grey matter of the spinal cord and the ganglia to the sensory organs and those of movement. This primary system is fundamental; it is the compulsory route followed by the exchanges which (from the nervous point of view) take place between us and the external medium; it may be sufficient in itself and be functionally active, as alone happens in reflex acts properly so called; it is even capable of preserving the impulse in itself by a kind of neuro-muscular circulation, as has just been described.

(b) *Superior Arc.*—The superior system is fed (as regards stimulation) by the preceding; it prolongs it into the interior of our bodies, and complicates it extraordinarily in doing so. The most ordinary observation teaches us that its capacity for stimulation is almost infinite. It represents, as regards stimulation, a reservoir which is almost inexhaustible. It also stores excitations internally, and this conservation is the first condition of the continuity of the psychical life (conscious or unconscious), and especially of the memory. We know that this psychical life can continue, and even be very intense, apart from every external stimulus and from every reaction against the external world; it is, therefore, concentrated in the superior parts of the nervous system, chiefly in the brain.

Their independent functional activity.—Clearly the superior system, both as a whole and its parts, is capable of isolation like the inferior; which means that, having received from this last a certain provision of impulses, it lays them up in itself before surrendering them to it.

The mechanism of this conservation is in principle the same as that which we

have seen in operation in the inferior system: it is effected by an automatism in virtue of which the impulse, after having traversed its paths, returns once again to them by a sort of continuous circulation. Indeed, *anatomy shows* us here, again, *the existence of a genuine closed circuit*, instead of the open arc which is generally accepted.

Their cyclic form.—The brain and the spinal cord are formed, as is well known, of white tracts and of grey masses. The white tracts are composed of fibres whose direction is opposed, some ascending, others descending, the first called *sensory*, the second *motor*, by analogy with the functions of the medullary root. These fibres, which are independent and isolated throughout their course, come into relation with each other in those localities which are occupied by the grey matter. This relation has been clearly established in the cerebral cortex between their superior extremities, and physiology makes use of it in order to explain the passage of the impulse from the first to the second; but this is not all: a connexion of the same nature has been proved to exist between their inferior extremities. The circuit postulated in order to explain the conservation of the impulse has, anatomically, a real existence.

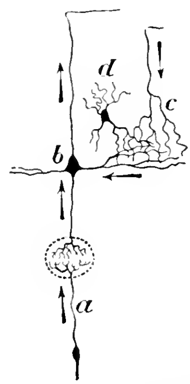


Fig. 108.—Peripheral reflection of impulses.

a, olfactory cell transmitting the impulse to the interior of a glomerulus; *b*, mitral-cell of the olfactory bulb collecting this impulse by a special protoplasmic prolongation forwarding it to the brain; *c*, axis-cylinder terminations of a neuron bringing back the impulse from the brain to the same mitral cell *b*, which collects it by a distinct protoplasmic prolongation; *d*, associationing cell.

The current of impulses proceeds in the direction of the arrows. From *a* to *b* the stimulation from the exterior penetrates to the interior of the nervous system. From *c* to *b* the impulse circulates in a cyclic system.

Inferior closure of the circuit.—The impulse, we say, is communicated from the ascending to the descending fibres (from the sensory to the motor fibres); this communication is obvious in the cerebral cortex; but fibres also pass from descending to ascending tracts: this communication is recognizable in certain sensory organs, especially in the retina, the olfactory bulb, the nuclei of the acoustic nerve. The optic nerve is not made up solely of ascending fibres (centripetal), but it also contains descending fibres (centrifugal), whose terminal ramifications are exhausted in the thickness of the retina. The impulse which the ascending fibres have once carried to the brain is collected by the descending fibres, near its point of departure, and, by the connexions that these fibres have with the ascending fibres of the optic nerve, it is once again carried into its first direction. There is a periodical and automatic renewal of the impulse.

In the olfactory bulb the same arrangement holds good, but with the interesting detail that here the arborizations are distinctly seen, those, namely, which collect the descending impulse in order to keep it in the circuit. The mitral cells of the olfactory lobe present, indeed, in addition to their axon, which is directed towards the brain, two kinds of prolongations.

Some of them, vertical in direction, receive the external stimulus transmitted by the primary olfactory neuron; others, extending laterally, are connected with the centrifugal fibres of the olfactory lobe (Van Gehuchten). It is these which assure the circulation of the impulses in the system.

The demonstrative value of these examples lies in the fact that, in the extremity of the centrifugal descending fibres the impulse has no possible connexion with the organs of movement; we cannot then suppose, considering the known properties of nerve elements, that it can have any other possible destina-

tion than to re-ascend towards the brain. The cycle is thus completed without the interposition of foreign elements. *The circulation* here is no longer neuromuscular; *it is internal to the nervous system itself;* it is a genuine *nerve circulation.*

Absence of Experimental Proof.—Our experimental methods, it must be admitted, do not permit us to observe this phenomenon of nerve circulation *in actu.* Nervous activity, indeed, is not discernible in itself, and the only available evidence of its existence that we possess is muscular movement. But, on the other hand, the contrary supposition, that the impulse never passes from the descending to the ascending fibres (a supposition which lies at the foundation of all the actual theories of nerve function) is not confirmed by any experimental fact which proves this impossibility. That the cerebral reflex arc exists, is universally allowed; is it open or closed at its inferior extremities? Experiment is silent on this point. But if we reflect that anatomy shows us at its inferior extremity, between its paths, connexions altogether similar (except that the relationships are inverted) to those which exist at its summit, the hypothesis that by these connexions a transmission of the impulse from the one to the other is rendered possible, as in the brain, is certainly plausible and may be maintained.

D. CLASSIFICATION OF NERVES

A methodical and analytical classification of the nerves according to their functions implies a knowledge of these functions which, at the present time, we are far from possessing. However, in proportion as the relations which the nervous system forms with the principal acts of the organism have been comprehended an effort has been made to distinguish and define them, by imposing upon them certain names. The result is that a *nomenclature* has been constructed whose terms are more or less justifiable and the sound foundation of which it is necessary.to discuss.

Remark.—A nerve is not designated according to the nature of its intrinsic activity (which we imagine, indeed, to be uniform in all the nerve elements), nor even from the nature of the phenomenon by which, at its termination, it acts on the elements to which it is distributed (which termination may also vary according to the nature of the element influenced, but is entirely unknown as regards its mechanism). *All nerves* without exception, all the species of nerves which are distinguished the one from the other, *are denominated according to the nature of the activity which they arouse in the elements which they immediately or mediately govern,* according to circumstances. These designations, which regard, the one extrinsic but neighbouring function, the other remote function, may lead, unless care is taken, to confusion and to double meaning.

Here are the principal characters which may be recognized in accordance with what is at present known.

1. Initial and terminal neurons.—Sensory and motor nerves.—In

following the nerve roots in the direction of the impulses which traverse them, *initial neurons*, which carry the impulse from without to the nervous system and arouse sensation in the latter, are met with ; these are obviously *sensory ;* at the other extremity *terminal neurons* are found, which convey the impulse to the muscles from the nervous system ; these are clearly *motor*. Between the one and the other *intermediate neurons* are interposed, forming what is known as the central nerve mass, as opposed to the roots which have just been referred to. Conventionally, this mass of intermediate *or associating* neurons is divided into two portions, or two collections of fibres, the one still called sensory, because they follow the roots of this denomination, the others motor because they end in the motor roots. But a reserve must be made concerning the applicability of these designations, and concerning the identification which would be effected between them and their homonyms the roots, as will be immediately seen.

(a) *Sensory varieties.*—The sensory nerves (initial neurons of the skin and of the sensorial organs) are thus named from the altogether *internal* phenomenon of *sensation* to which they give rise in the sensory or sensorial systems of which they form the gate of entry, and which are situated in the so-called central mass, intermediate between them and the motor roots. In this category of sensory nerves, as many subdivisions and species as there are distinct senses may be defined ; each is definite, both as regards the nature of the excitation of the given sense, and that of the sensation to which it gives rise, that is to say, of the systematic function which comes directly after it (optic, acoustic, tactile, gustatory, olfactory nerves).

(b) *Motor varieties.*—The motor nerves (terminal neurons) are also named after the external phenomenon of movement which they initiate in the cells with which they come in contact by their termination.

Unlike the sensory nerves, which ensure the accomplishment of a systematic function, they give rise to a purely cellular function (contraction in the muscular elements ; secretion in the elements of the glands, etc.). They are divided naturally into categories corresponding to these functions (*motor* nerves properly so called, *secretory* nerves, etc.).

2. Intermediate neurons.—The preceding designations are both comprehensible and legitimate ; the problem to be solved is, further, relatively simple when it is a question of the two varieties of the preceding nerves ; because, being placed at the entrance to and exit from the nervous system, they permit us to see more clearly their connexion with the exterior, which remains our criterion. Very great difficulties arise when it is a question of the neurons of the intermediate mass

and when we endeavour to effect a classification of them which is based on their functions. Being internal to the nervous system itself, without direct connexion with the peripheral organs for the reception of the stimulation or of the execution of movement, we are deprived of the two methods which have served us above for choosing and justifying our designations.

They receive the impulse from other nerves which precede them, and they restore it to yet other nerves which follow them. Their function is thus to transmit the impulse from one nerve element to another. Either as regards the manner in which they receive this impulse, or as concerns that in which they transmit it, there is no doubt that they must present differences amongst themselves, of which the initial and terminal neurons furnish us with an imperfect example, but which are certainly still more obscure. However, positive facts teach us that this transmission may have, as regards the activity of the neurons, two very different and opposed results.

The impulse transmitted from one neuron to another may have the effect : (a) *of eliciting its activity*, (b) *of reducing it to inactivity*. These two effects are clearly exclusive the one of the other, and are observed in circumstances peculiar to each case.

Exciting and inhibitory neurons.—The intermediate neurons may then have, as regards the neurons with which they come into connexion, two different functions by which they may be divided into two distinct classes. Some give rise to activity, and elicit the function of those which follow them : they may be called excito-functional or simply exciting, since we in no way assume the function which they stimulate. The others interdict the functional manifestations of the nervous paths which follow them : they may be called inhibito-functional or simply *inhibitory*, in opposition to the preceding.

The activity, whether of transmission or of hindrance to the transmission of impulses which corresponds to the most general function of these neurons, is capable of being decomposed into a certain number of secondary functions, comprising the modalities, certainly diverse, according to which this positive or negative transmission is effected under particular circumstances.

These modalities we can but suppose to concern the *direction*, the *conflicts* and, generally speaking, the *connexions* impressed on the impulses in the complicated systems of neurons which form the strictly nervous portion of the nervous system.

At the present time our methods of analysis do not supply us with any means of directly determining the actions exerted by one nervous element on another nervous element. The little that we know of the

latter is indirectly furnished to us by the ultimate evidences of nerve action (organs of the movements executive of functions).

3. **Functional systems of neurons.**—Another source of difficulty in the classification of nerve species lies at the very foundation of the subject; I mean, it arises from the complexity of the laws which govern the organization of nerve elements in hierarchically superposed systems, which are, each in turn, constituent portions the one of the other. A nomenclature founded on dichotomic distinctions, analogous to botancial or zoological classifications, is, however, insufficient to give an idea of such an organization. The divisions and subdivisions of the nervous functions, when they are exactly known, will not be spread out on the same plane, but will extend in many directions.

The first distinction to be made is not to confound, but, on the contrary, to separate the functions which belong to elements from those which belong to aggregations; to distinguish cellular functions from systematic functions. Some definite examples will make this difference clear.

Examples.—The phrenic nerve is the motor nerve of the diaphragm. For this purpose it transmits to the latter an impulse in order to bring about its contraction in all the functions in which this muscle participates. As is the case with the greater number of muscles, these functions are multiple. As regards the diaphragm, at least two may be mentioned: the ventilation of the lung, and the swallowing of aliments. The diaphragm, during respiration, draws air into the chest; in swallowing, it draws the alimentary bolus into the œsophagus. In the first case, the action is associated with that of a certain number of the thoracic muscles which take part in the performance of respiration, in inspiration; in the second, it acts together with the buccal muscles, and the pharyngeal and the œsophageal muscles, which perform the act of deglutition. These muscular connexions and those of the neurons which directly control these muscles are effected in the nervous system, namely, in that portion of it which is intermediate between the motor and sensory nerves, properly so called, and which is formed of the neurons known as those of association. In order to perform the function of deglutition, the phrenic nerve enters into a complete and definite system; for its performance of respiration, it enters into another equally definite system. It is not the phrenic nerve which is respiratory, as has been sometimes said, but rather the system to which it belongs at the instant of its performing the function which this system subserves.

The hypoglossal nerve, by the muscles which it supplies, may also take part in the performance of several different functions: mastication, deglutition, articulate speech, etc. And this is also effected by the connexions which it forms with other nerves supplying other muscles; associations which, according to their degree of importance and complexity, are effected between the neurons of the bulbar, peduncular or cortical region of the nervous system. To be accurate, the reasoning does not apply to the hypoglossal, a bundle of neurons taken together, but to each component neuron of this nervous bundle.

The same remarks would apply to the facial and other motor nerves. These remarks are self-evident, but they deserve nevertheless to be emphasized. The expressions respiratory nerves, nerves of phonation, nerves of expression and such

like, are only exact when it is understood that these epithets are transposed from the terminal nerve, to which they are customarily applied, to the whole which performs the function thus designated.

In the preceding example, it is a question of movements carried out in the same situation and by the same muscles, movements which, according to their degree of complication, require a systematization in itself more or less complicated and extended in the nervous system. If we now consider movements carried out in different and apparently independent localities, the systems which co-ordinate them perform their functions, to a certain degree, independently the one of the other; but this independence is scarcely ever absolute. Between juxtaposed or parallel systems bonds of union exist, sometimes close, sometimes lax, by which they interpenetrate, and thus secure, amidst incessant variety the unity of the nervous system. Further, it must be understood that their limitation, such as we conceive it in order to describe them, is in a great degree arbitrary; it corresponds in each case to an external phenomenon of movement which we have ourselves conventionally limited for the purpose of analysis. Instead of definite limits separating distinct nervous territories, it is rather a progressive laxity of the bonds of union between neighbouring elements and systems the existence of which must be admitted in order to faithfully represent the condition. It must be added that these boundaries, thus vaguely pointed out, change at every moment, according to the variations of function.

4. The centres.—This organization of nervous elements into systems and sub-systems of varying complexity which excite and co-ordinate functions should, in our opinion, be substituted for the conception of centres, on which has been conferred, by *a priori* reasoning, this power of excitation and co-ordination. If, however, as is the custom, the term "centre" is applied to those regions of the grey matter in which the anatomical and functional bonds of union between elements and systems are established, this expression may be maintained; but it is necessary to confine the idea which it implies to that of the connexions which, in the grey matter, exist between the components of the systematic aggregations. This definition does not correspond to the etymology of the word, but it represents the exact truth. In fact, we see that those areas of the grey matter which are known as centres are the more extensive and more numerous in proportion as the function is higher, and as its movements are more complex and, it may be said, more spontaneous. These so-called centres are one of the important conditions of the systematization: they explain it to us.

To take an example, the vaso-motor nerves (that is to say, nerves of the circulation) form a system of this kind which is simpler than the preceding ones, whose associating neurons extend outside the vertebral canal, towards the ganglia of the great sympathetic. This last seems clearly to be a systematized assemblage of neurons which preside, not merely over the circulation, but also over other analogous functions.

1. The nervous system and heat. The thermic nerves

Cellular activity declares itself very generally by more or less apparent movement ; it is rendered evident still more generally by a development of heat. The muscle which contracts, the gland which secretes, both become warmer, the one more than the other, but both to a sensible degree. This development of heat is, like movement itself, an evidence of the activity of the organs and, indirectly, of the nerves which preside over them. The motor (or secretory) nerves are, then, from the very fact that they are motor, thermic or calorific nerves. The inhibitory nerves are those which hinder, not only the occurrence of movement, but also the disengagement of heat. They should not be called *frigorific*, as they have sometimes been described, because in reality they do not cause the absorption of the external heat by the organs, but only hinder the latter from producing it.

1. **Cellular exciting function of disengagement of heat.**—However this may be, the disengagement of heat being the most general phenomenon of the activity of the cell, there is no nerve which either directly or indirectly does not influence thermogenesis. On the other hand, this development of heat being, like movement itself, merely one of the aspects of cell function, it follows that all the nerves which directly or indirectly give rise to movement, are hence thermic nerves ; and reciprocally, there are no thermic nerves but those which influence movement. In other words, *the thermic nerves are not distinct from the motor nerves,* but are merely these latter nerves regarded from the point of view of their connexion with heat, instead of with movement, the two things being, in fact, merely two different aspects of the same function.

2. **Systematic regulative function of temperature.**—From the cellular point of view, the function of the thermic nerves is confounded with that of motor nerves. But it is none the less true that (in the superior vertebrata) there is a *function for the regulation of heat,* and this function makes use of a special system of co-ordinated nerves in order to obtain a fixed temperature ; a system in which the nerves strictly called motor only partially enter with the purpose of increasing or diminishing, according to circumstances, the heat produced, together with other nerves which increase or diminish, also according to circumstances, its loss by the skin and lung, in such a way that this fixed thermic level may be maintained by compensations in spite of the variations of external temperature.

This is one of the most cogent examples of the *dependence of the part on the whole, and of the whole on the part,* which is one of the characteristics of the animal organization.

The systems which, by the association of elements in a determinate order, execute those functions on which life with all its various manifestations depends, should not be considered as juxtaposed and entirely independent aggregations. Indeed, they are included the one in the other, as the part is in the whole. It is thus that the system which subserves the emission of a cry is included in that which presides over phonation, reflex articulation, thought out language and that which is the result of reflection. The first is practically the foundation and point of departure of the others, which are formed by successive additions, whose highest portion is located in a definite region of the cerebral cortex.

2. The nervous system and nutrition. Trophic nerves

Among the phenomena whose relation to the nervous system is determined by observation and experiment, there are some simple, as heat and movement ; but there are also others which are complicated and much more vaguely defined, such as those which are included under the general name of *nutrition*. In acting on the nervous system, heat is given off, and we have seen that this action does not imply the existence of special nerves conveying a specific influence to the cells, but that it is confounded with the general stimulation of the cells by the motor nerves. By acting on the nervous system, the nutrition of the tissues under the influence of nerves may also be disturbed, and it is necessary to point out that this perturbation is once more merely a consequence, more remote, indeed, of the want or excess of functional activity (according to circumstances) which follows the nerve alteration, and is not a specific influence, conveyed to the cells by anatomically distinct nerves, such as trophic nerves would be.

In principle, this tendency to admit as many varieties of nervous action as there are of relations between the nervous system and the organs which depend on it, is unscientific, and reasoning easily proves that it is ill-founded.

1. Immediate and consecutive influence of the nervous system on the Tissues.—Alteration of the muscles.—Section of the nerves which supply the muscles causes the *immediate* paralysis of the latter, that is to say, the cessation of the disengagement of energy (heat and mechanical work) by which their activity is manifested. And a further *remote* consequence is a structural modification of the muscle fibre, which loses its histological characters and atrophies ; *this atrophic degeneration is a consequence of the permanent loss of activity of the muscular element.* Three conditions are essential to the cellular life : a fresh supply of nutritive substance, supply of energy (which is indeed allied to this substance), supply of the stimulus which makes use of this energy and of this matter ; if one only of these conditions be wanting, the cell will be in danger ; it is a general law of which this is only a particular instance.

2. **Alterations of the skin and of the cornea.**—Section of nerve trunks which are in connexion with the skin or the cornea equally brings about, after a certain time, alterations of these structures (opacity, ulceration, etc.). These disturbances of nutrition have been and still are one of the strongest arguments appealed to by those who maintain the existence of an independent species of nervous activity, specifically trophic; and the force of the argument lies in this, that nerves analogous to the exciting nerves of the muscles are not known to be distributed to the skin or to the cornea in order to provoke and govern the functions of these organs. But this arises doubtless from the fact that this function, itself of a chemical or molecular nature, eludes our means of authentication, and does not manifest itself by anything immediately obvious at the moment of the section or the stimulation of the cutaneous or corneal nerves. The structure is not less gravely altered by lesion of nerves which preside over it, and this alteration is only made manifest by its remote effects, that is to say, by the structural degeneration which is the necessary consequence of the perversion of function.

In short, the so-called *trophic nerves are not only*, like the so-called thermic nerves, *those which promote the special function of the organ to which they are distributed*; they are, histologically speaking, the same fibres. It must be assumed that these exciting nerves are distributed to all the fixed elements of the organism, at any rate to the greater number of them. Where the function is obvious, they appear to be both excitors of function and regulators of nutrition. Where the function is unknown or dissimulated, they appear only as trophic nerves. It is this which has given rise to the belief that these are distinct and independent nerves specially devoted to nutrition.

Unity of function and unity of cell excitation.—As regards a given single nerve element, there only exists a single order of neuron; that, namely, which arouses the special function of the element. In this function, relatively simple (cellular function), but having multiple and divers aspects, everything is closely connected; the excitation or the non-excitation to which we subject it by our experiments on the nervous system causes the development of a consecutive series of phenomena suggesting those which are the result of its normal or even pathological activity. The bond of union which gathers together these phenomena under a common dependence, and gives to each cell its functional unity, has nothing to do with the nervous system; it is internal to the cell itself, very different from that which organizes the functional systems and which, effected between the elements of the system, is located in its turn internally to the latter. To return to the nature of the nerve action by which this bond of union between the elements in the constitution of the systems is realized, we repeat that it is univocal; it can be only excitor or inhibitory; it either causes the evolution of functional manifestations in their regular succession, or it hinders their production whatever they may be; it regulates neither their nature nor their particular direction. It is a provoking cause, it is not an efficient cause.

3. The nervous system and animal chemistry

The trophic disturbances which result from the functional alterations of the nervous system have diverse ways of displaying themselves, such are: atrophies, hypertrophies, deviations of the external form of apparatus and organs, all directly appreciable to observation. These *macroscopic* changes are caused by *microscopic* alterations of the component cells of these parts. If we carry the analysis farther, we see that these so-called elementary alterations depend, in their turn, on structures of a still more elementary character, internal to the cell, in a word *molecular*, and which are thus the foundation of the organization of the living being. These molecular structures are nothing else than those which chemistry studies by its appropriate methods when it desires to examine the constitution of different substances, from simple bodies up to albumen, for example.

The degrees of organization.—The organization of the living being thus forms a continuous and regularly graduated series, whose point of departure is situated in the chemical elements; to interfere with this series is to compromise the entire edifice; to maintain it in its integrity is one of the conditions essential to its persistence and its solidity. It is for this reason necessary to examine the connexions of the nervous system with animal chemistry.

Convergence of the phenomena.—Between a tissue thus highly differentiated and structures of molecular order (that is to say, the most inferior), the connexions are not evident at the first glance. They are better understood if it is remembered that the molecular phenomena, internal to the cell, are mutually subordinated, cyclic, converging towards a definite end, and that their final result may thus be as simple as their mechanism is complicated. Two cellular elements, two organized systems, may thus possibly react on one another in a very simple manner. The stimulation of the tissues by the nerves is an act of this kind. Very simple in itself, it is, as regards the stimulating tissue, the initial phenomenon of another equally complicated series of cyclic and convergent acts.

Nutritive equilibrium.—Trophic disturbances are revealed to us by a change in the form and structure of organs. It is necessary to remember in this connexion that the structure, molecular (or otherwise) of these parts is not a static condition, but that the persistence of their forms marks an incessant renewal of the organized substance.

This persistence is the index of the regularity of this renewal. From the fact that the structure of the organs depends on an equilibrium which is thus perpetually mobile, a directing influence is necessary which is capable of effecting between the forces which co-operate in it the compensations required to maintain it within its correct limits; and the nervous system, so far as regards the functions with which we are acquainted, appears to us, once again, to be the most appropriate to assume this directive and regulative influence.

The actions of the living being take their first origin in the chemical reactions of its substance. The nervous sysetm, when it intervenes, only influences these actions through the intermediation of these chemical reactions. What is the nature of the influence which it has over them? But first of all, what are the reactions themselves? How are they arranged?

Reactions of the organism.—Some of these reactions are *reversible*; the others, *irreversible*.

(a) *Reversible reactions.*—A phenomenon is called reversible when it consists in *a change, or in a series of changes, which may take place in either direction from the initial to the final condition, and from the final to the initial condition, by passing precisely the same intermediate stages.* Example: oxygen and hæmoglobin being submitted (under uniform conditions as regards temperature)

to increasing pressure, a compound will result, oxyhæmoglobin, whose quantity is in a direct relationship with this pressure. If the pressure continuously decreases, the quantity of oxyhæmoglobin will decrease, following the same curve, but in an opposite direction. There is thus in the one case association and in the other dissociation of the two components, and hence it is said that oxyhæmoglobin is a *dissociable* combination.

(b) *Irreversible reactions.*—A phenomenon is irreversible when it consists in *a change or a series of changes which can only take place in a determinate direction, in such a way that, in order to return to the final from the initial condition, it is necessary that a different cycle be followed from that taken in proceeding from the initial to the final condition.* Example: from the glycogen which is burnt in contact with oxygen, carbonic acid and water are formed; but we do not know of any means by which this process can be inverted (nor even any means in the domain of ordinary chemistry) of reproducing glycogen and oxygen with this carbonic acid and this water. The formation of glycogen, on the one hand, and its destruction on the other, are irreversible reactions.

Chemical equilibrium.—From the point of view of energy, reversible and irreversible reactions differ profoundly.

(1) **In reversible reactions.**—In the first the *chemical equilibrium is constant and stable;* according, indeed, to the state of the temperature and of pressure, combination occurs or is resolved in the proportions desired in order that this equilibrium may also be satisfied. In such combinations the bodies do not acquire any reserve of energy or any potentiality.

(2) **In irreversible reactions.**—In the second it is not so: the complete cycle of the phenomenon, starting from a given initial condition in order to return to this initial condition, manifests indeed in its turn two orders of reactions which are inverse, but not symmetrical, as is the case with the first.

(a) *Ascending phase.*—In the first phase, the reacting bodies absorb and accumulate in themselves a certain quantity of energy which is connected with the particular position which their molecules assume within them: the reaction is then called *endothermic.* Example: the radiant solar energy is absorbed by plants for the synthesis of starch; the molecules of the body thus produced are in *unstable equilibrium,* the energy accumulated in it to give the molecules their particular position, is always ready to be expended in order to make them leave this position and destroy this body by giving rise to new combinations. The energy thus stored up is called its reserve or potential energy; the body is called explosive.

(b) *Descending phase.*—In the second phase, this unstable equilibrium is destroyed: the molecules lose their relative situation, new combinations make their appearance, the energy held in reserve becomes free and is manifested in the form of heat or of mechanical work: the reaction is then called *exothermic.* Example: starch (or glycogen) in contact with oxygen is transformed into carbonic acid and water, with disengagement of all the radiant energy which has been absorbed by the plant in order to produce this combination.

Rupture of equilibrium.—The irreversible cycle differs, as is obvious, from the reversible cycle, inasmuch as it has a definite direction of which the different stages can be recognized. An *ascending* phase can be determined, during which energy is stored up, and a *descending* phase, or that of expenditure of energy. Between the two occurs the phenomenon of rupture of molecular equilibrium, and this opens the second phase.

Energy of disengagement.—This rupture of equilibrium requires the intervention of an energy which, from the time of Helmholtz, has been known as the *energy of disengagement.*

Direct nervous action.—The following principle may be regarded as indis-

putable: *the nervous system can only have a direct action on the exothermic reactions of the organism;* that is to say, on the irreversible reactions which give off energy. Itself representing an infinitesimal amount of energy (energy given off), it can only have a directly efficient action in overcoming an unstable equilibrium. Its duty is to cause an expenditure of energy, not to supply it to the tissues. Energy arises by another route; it is supplied by the aliments which have been stored up, and which the circulation distributes to these tissues in the form of somatic or cellular reserves.

The comparison of the *ingesta* with the *excreta* well shows this *alimentary origin* of energy. The heat of combustion of the first is considerable, that of the second is almost *nil;* the difference between the two precisely measures the quantity of energy which the animal organism gives off in the course of the transformations which the first undergo in order to become the second. It is the duty of the nervous system to control and to direct this expenditure of energy, by exciting the transformative reactions by means of which the excreta are derived from the aliments.

Syntheses in animals.—If, however, these transformations, in their totality, follow a general curve which may be called descending, it is not less certain that, from their initial state (aliments), to their final condition (excreta), they present certain oscillations in the course of which energy is now liberated, now absorbed, before being finally almost totally expended. Alongside of these analytical reactions which characterize animal chemistry in the general cycle of the living kingdom (vegetable and animal), there are synthetic reactions which take place in the animal resembling, if not identical with, those which occur in the vegetable.

Indirect nervous action.—In the animal which possesses a nervous system, as in the vegetable which possesses none, these synthetic reactions elude the *direct* action of this special system.

(a) *On the irreversible endothermic reactions.*—Nevertheless they may, in an *indirect* manner, fall once again under its influence, in the sense that the portion of the energy rendered free by the exothermic reactions may be utilized *in situ* for the performance of endothermic reactions which require an unappropriated energy in order to be carried out. The heat given off by the cells during their functional activity would here perform the office of the solar radiations by which the syntheses of vegetables are effected; and thus would be explained the intimate bond of union which exists in the cells between the expenditure of energy of which they are the seat and the re-accumulation of their available reserves in proportion to their exhaustion.

(b) *On the reversible reactions.*—As regards the reversible reactions, inasmuch as their characteristic is that of presenting a constant molecular equilibrium, the energy of disengagement which circulates in the nervous system has, in their case, no hold on them. Where equilibrium is stable, there can be no rupture of equilibrium. But these reactions may equally, like the preceding, fall once again under the influence of the nervous system in a roundabout way; for this to be so it suffices that the conditions of temperature and of pressure on which they depend, be themselves changed through nervous action, that is to say, as the direct consequences of this action.

Example.—This is what happens in the muscle, when, as the result of the stimulation of its nerve, the oxygen contained in its plasma acts on the glycogen in order to burn it up; the condition of the temperature is not markedly changed, but the tension of the gases is considerably so. The glycogen, in order to be transformed into carbonic acid, absorbing the oxygen of the muscular plasma, consequently lowers the tension of this gas in the liquid intracellular medium. Hence the muscular hæmoglobin, then the hæmoglobin of the blood, are dissociated. Carried away by the venous blood, this hæmoglobin finds in the lung

a pressure of oxygen sufficient to reproduce the oxyhæmoglobin combination which has been destroyed in the muscle, and this, in its turn, carried away by the arterial current to the muscle, will again be destroyed in it, and so on.

Initial phenomena.—The point of departure of these changes is not located in the lung, as seems often to be thought, but rather in the tissues, and *the initial phenomenon is a nervous excitation* whose consequences are gradually felt throughout the economy, indirectly it is true, but inevitably.

BIBLIOGRAPHY

Reflex Movements ; Reflex Power.—Beaunis, *C. R. Acad. sc.*, 1883, p. 841.—Beyer, *Arch. gén. de méd.*, 1834.—Brown-Séquard, Physiol. comparée, *Biologie*, 1849 et 1857.—Calmeil, *Journ. des progrès*, 828, t. XI.—Carpentier, Principles of Physiology, éd. 3, London, 1851.—Danileski, *Arch. f. d. ges. Phys.*, 1892, Bd. LII.—Debrou, *Arch. gén. de méd.*, 1847, t. XV, p. 222.—Flourens, Fonct. du syst. nerveux.—Fodera, *Journ. de la physiol. exp.*, t. III, p. 214.—Freusberg, *Arch. v. Pflüg.*, 1874, t. IX, p. 358 Van Gehuchten, Le mécanisme des mouvements réflexes, 1897.—Gergens, *Arch. v. Pflüg.*, 1877, t. XIV, p. 340, et 1876, t. XIII, p. 61.—Grainger, Functions of spinal Cord, London, 1837.—Goltz . . . Nervencentra des Froscher, 1869.—Helmholtz, *Monatbl. Berl. Acad.*, 1864.—Hering, Uber. d. Gedächtnis als allg. Funct. d. organisirt Materie, *Sitz. d. k. Acad. d. Wiss. Wien*, 1870.—Lallemand, Obs. path. propr. à éclair. plus. points de physiol., Dissert. inaug., Paris, 1818.—Legallois, *Œuvres*, Paris, 1830, t. I.—Loeb, *Arch. f. d. ges. Phys.*, 1894.—Marshall-Hall, *Philos. Trans.*, 1833 ; *The Lancet*, 1838 ; *Ann. sc. nat.*, série 2, 1837, t. VII ; Aperçu sur le syst. spin., Paris, 1855.—J. Müller, *Manuel de phys.*, t. I, p. 608 (trad. Jourdan).—Os. Naumann, *Arch. v. Pflüg.*, 1872, t. V, p. 196.—Pflüger . . . Zeistungesetze d. Reflexionen, 1852.—Prochaska, Operum minorum anat. phys. et path. argum., Viennæ, 1800.—Vulpian, Leçons sur la phys. comp. du syst. nerv.—Walton, *Arch. f. Anat. und Phys.*, 1882, p. 46.—Ward, *Arch. f. Anat. und Phys.*, 1880, p. 72.—Whytt, On the vital and the other involuntary motions of animals, Edinburgh, 1750.—Wundt, Ub. reflex. org., 1876.

Inhibition of the Reflexes.—Albertoni, *Arch. ital. de biol.*, 1887 ; Ch. Bernard, Leç. sur le syst. nerv., Paris, 1858, t. I, p. 378.—Brown-Séquard, *Arch. de phys.*, 1879, p. 495.—E. Cyon, *Beiträge z. Anat. und Phys.*, 1875.—Gluge, Inhib. des mouv. rythm. du sphincter, *Bull. Acad. Roy. Belg.*, 1868.—Goltz, *Arch. f. d. ges. Phys.*, 1873.—A Herzen, *Unters. z. Naturlehre*, t. IX.—Langendorff, *Arch. f. Anat. und Phys.*, 1877 p. 96 ; 1877, p. 435.—P. Marie, Leçons sur les maladies de la moelle, 1892.—Nothnagel, *Centralbl.*, 1869.—Ris. Russel, *Brit. med. Journ.*, 1896.—Schlösser, *Arch. f. Anat. und Phys.*, 1880, p. 303.—Setschenow, *C. R. Acad. sc.*, 1863 ; *Arch. v. Pflüg. f. Anat. d Phys.*, 1880, p. 303.—Setschenow, *C. R. Acad. sc.*, 1863 ; *Arch. v. Pflug.* 1875, t. X, p. 163 ; *Zeit. f. rat. Med.*, XXIII et XXVI.—Simonoff, *Arch. f. Anat.*, 1866, —Spode, *Arch. f. Anat. und Phys.*, 1879, p. 113.—Tarchanoff, *Arch. f. d. ges. Phys.*, 1887, Bd. XL, p. 340.—Weil, *Centralbl.*, 1871.

Fragmentary Reflexes.—Bethe, *Arch. f. d. ges. Phys.*, 1897, Bd. LXVIII.—Goltz, *Centralbl. f. d. Wiss.*, Berlin, 1866.—Herbert Mayo, Anat. and Phys. Comment., London, 1823, vol. II.—Masius, *Mém. Acad. Roy. de Belgique*, 1870, t. XXI.—Sherrington, *Phil. Trans.*, 1893, vol. CLXXXIV, p. 641.

Tonus : Contractions.—Bischoff, *Wien. klin. Woch.*, 1896.—Bouchard, *Arch. gen. de méd.*, 1866.—Brondgeest, *Arch. de Du Bois-Reymond*, 1860, p. 703.—Bruns, *Arch f. Psych.*, 1893, XXV.—Van Gehuchten, *Journ. de neurol.*, 1897 et 1898.—Mann, *Neurol. Centralb.*, 1898.—P. Marie, Leçons sur mal. de la moelle.—Marinesco, *Sem. méd.*, 1896, p. 214, et 1898.—Verworn, *Arch. f. d. ges. Phys.*, 1896.

Medullary Reflexes.—A. Bickel, *Arch, f. d. ges. Phys.*, 1892, Bd. LII.—Hallstein, *Arch. f. Anat. und Phys.*, 1885, p. 167 ; 1886, p. 92 et p. 500 ; 1887, p. 316 ; 1888, p. 163, —Loeb, *Arch. f. d. ges. Phys.*, Bd. XLIX.—Meihnizen, *Arch. v. Pflüg.*, 1873, t. VII, p. 201.—Mendelssohn, *Sitz. d. k. pr. Acad. d. Wiss.*, 1882, 1883, 1885 ; *Congrès de neurologie de Bruxelles*, 1897.—J. Ott, Dil. pupill., *Journ. of Phys.*, 1879-80, t. II, p. 443. —Rosenthal et Mendelssohn, *Neurol Centralb.*, 1897.—Sanderz-Hezn, *Arb. aus d. phys. Anat. z. Leipzig*, mit. geth. d. Ludwig, 1867.—Sherrington, *Phil. Trans.*, 1897, Textbook of Physiol. of Schäffer.

Tendon Reflex.—Barbé, *Biologie*, 1889.—Brown-Séquard, *Journ. de la phys.*, 1858. —Bouchard, *Arch. gén. de méd.*, 1866.—Brissaud, Recherches physiologiques, 1880. —Charcot et Joffroy, *Arch. de phys.*, 1869.—Gotch, *Journ. of Phys.*, 1897.—Heller, *Berl. klin. Woch.*, 1886.—Hug. Jackson et R. Russell, *Brit. Med. Journ.*, 1893.—Jendrassik, XIII[e] Congrès int. de méd. Paris, Neurologie, p. 155.—Joffroy, *Arch. de phys.*, 1881, p. 474.—Lombard, *Americ. Journ. of Phys.*, 1888 ; *Arch. f. d. ges. Phys.*, 1889, suppl. p. 292.—Meyer, *Berlin. klin. Woch.*, 1888.—Weir-Mitchell et Lewis,

Med. News, Philad., 1886.—Muskens, *Neurol. Centralbl.*, 1899.—Plympton Lombard, *Arch. f. Anat. und Phys.*, 1889, suppl. p. 292.—Prevost, *Revue de la Suisse romande*, 1881.—Sherrington, *Journ. of Phys.*, 1892 ; *Proceed. Roy. Soc.*, 1892 ; XIII[e] Congrès intern. de méd. Paris, Neurologie, p. 149.—Schreiber, *Arch. f. exp. Path. und Pharm.*, 1885, Bd. XVIII, p. 270.—Teschirjew, *Arch. f. Anat. und Phys.*, 1880, p. 566.—Waller, *Journ. of Phys.*, 1890.—Westphal, *Arch. f. Psych.*, 1875.—De Watteville, *Brain*, 1886.

Cutaneous Reflex.—Babinski, *Biologie*, 22 fév. 1897 ; *Revue neurol.*, 1900.—Boeri, *Riforma medica*, 1899.—De Buck et de Moor, *Journ. neurol.*, 1900.—Cestan et Le Sourd, *Gaz. hop.*, 1899.—Van Gehuchten, *Journ. de neurol.*, 1897.—Remak, *Neurol. Centralbl.*, 1893.—Walton et Paul, *Journ. of nerv. and ment. dis.*, 1900.

Cremasteric Reflex.—Marandon de Montyel, *Arch. de phys.*, 1895, p. 571.

Respiratory Reflexes.—François-Franck, *Arch. de phys.*, 1890, p. 508.—Gad, *Arch. f. Anat. und Phys.*, 1881, p. 566 ; 1886, p. 388 ; 1890, p. 588 ; 1891, p. 335.—Joseph, *Arch. f. Anat. und Phys.*, 1883, p. 463.—Sandmann, *Arch. f. Anat. und Phys.*, 1887, p. 483.

Vaso-motor Reflexes.—Belfield, *Arch. f. Anat. und Phys.*, 1882, p. 298.—Couty et Charpentier, *C. R. Acad. sc.*, 1877, p. 161.—Cyon, *Arch. v. Pflüg.*, 1874, t. VIII, p. 327.—Dastre et Morat, Réfl. vaso-dilat. oreille, *C. R. Acad. sc.*, 1882, t. XCV, p. 929.—Dittmar, *Arb. phys. Aust. z. Leipzig*, 1870.—François-Franck, *C. R. Acad. sc.*, 1876, t. LXXXIII, p. 1109 ; 1879, t. LXXXVIII, p. 893 ; 1896, p. 179.—Heidenhain, *Arch. v. Pflüg.*, 1874, t. IX, p. 250.—Hallion et Comte, *Arch. de phys.*, 1895, p. 90.—Kabierske, *Arch. v. Pflüg.*, t. XIV, p. 518.—Kowalewsky et Adamuk, *Centralbl. f. d. med. Wiss.*, Berlin, 1868, p. 582.—Laffont, Reflex. Löven, *C. R. Acad. sc.*, 1882, t. XCV, p. 864.—Langley, *Phil. Trans.*, 1892 (bibliographie).—Luchsinger, *Arch. f. d. ges. Phys.*, 1878, Bd. XVI, p. 518.—Ludwig et Thiry, *Acad. d. Wiss.*, Wien, Bd. XLIX.—Margliano et Lusona, *Arch. ital. de biol.*, 1889, t. XI, p. 246.—Ranvier, *C. R. Acad. sc.*, 1892, t. CXIV, p. 629.—Stefani, Act. vaso-motrice ; réflexe de la temp., *Arch. ital. de biol.*, 1895, t. XXIV, p. 414.—Reid Hunt, *Journ. of Phys.*, vol. XVIII, p. 381.—Vulpian, Leçons sur l'app. vaso-motor.

Reflexes of the Great Sympathetic.—François-Franck, Art. "Sympathique" *du Dictionnaire* de Dechambre.—J.-N. Langley, *Journ. of Phys.*, 1894, vol. XVI, p. 410.—Gaule, *Arch. f. Anat. und Phys.*, 1892, suppl. p. 29.—Goltz et Ewald, *Arch. f. d. ges. Phys.*, 1896, Bd. LXIII.—Munck, *Arch. f. Phys.*, 1878.—Sokowin, Act. réfl. gangl. mésent. Beitr. z. Lehre d. Entleerung dex Harns, *Hoffmann und Schwalbe Jahrb.*, 1878.—Vulpian, Leçons sur les vaso-moteurs.—Wertheimer, *Arch. de phys.*, 1892.

Oculo-pupillary Reflex.—Chauveau, *Journ. de la phys. homme et anim.*, 1861, t. IV.—Stefani et Nordera, *Arch. ital. de biol.*, 1900, t. XXXIII, p. 305.—Vulpian, *C. R. Acad. sc.*, 1878, t. LXXXVI, p. 1436.

Various Reflexes.—Berger, Réflex .palpéb . . . anesthésie, *C. R. Acad. sc.*, t. XCIII, p. 971.—Cl. Bernard, Réflex. intest. Leçons sur le syst. nerv., 1858, t. I, p. 378.—Bickel, Défécation réfl., *Rev. méd. Suisse romande*, Genève, 1897.—Bochefontaine, Excit. dure-mère, 1876-83, p. 397 ; *Arch. de phys.*, 1873, p. 1.—Cyon, Contract. utérines, *Arch. f. d. ges. Phys.*, 1874, Bd. VIII.—Dastre, Réflexe labio-mentonnier, ultimum réflexe, *Biol.*, 1886.—Dejerine, Tremblem. réflexe, *C. R. Acad. sc.*, 1878, t. LXXXVI, p. 1274.—Fr.-Franck, *Arch. de phys.*, 1889, p. 538.—Goltz, Réflex. génit. *Centralbl. f. d. med. Wiss.*, 1865, et *Arch. f. d. ges. Phys.*, 1874.—Guinard et Tixier, *C. R. Acad. sc.*, 1897, t. CXXV, p. 333.—Alf. Haue, Réflex. contract. sur un muscle inhibiteur sur l'autre, *Arch. f. d. ges. Phys.*, 1899, Bd. LXXIII, p. 453.—Kocher, Erection, Mitth. a. d, Grenzgeb. d. Med. und Chir., Iéna, 1896, Bd. I, p. 556.—Langendorff, Réflexé croisé, *Arch. f. Anat. und Phys.*, 1887, p. 141.—Masius, Réfl. urinaire *Bull. Acad. Roy. sc. Belg.*, 1868.—J. Ott, *Journ. of Phys.*, 1879.—Ch. Richet, Somnambulisme, *Arch. de phys.*, 1881, p. 145 ; Paralysie et anesthésie réflexes, *Ibid.*, 1883, t. II, p. 367.—Schlesinger, Réfl. utérus. *Gaz. hebd. méd. et chir.*, 1872, p. 847.—Spallanzani, Opera sopra la riproduzione animale, Modena, 1768 ; Exper. sopra la gener. dei anim. e veget., 1875.—C. Stewart; Réfl. vésic., *Am. Journ. of Phys.*, Boston, 1899, vol. III p. 182.

Reflex Autotomia.—Jean Demoor, Trav. stat. zool. de Helder, 1891.—Léon Fredericq, *Arch. zool. exp.*, 1883 ; *Arch. biol.*, Gand, 1882 ; *Revue scientif.*, 1886 ; *Trav. lab. Marey*, 1887–88, t. II, p. 201.—Preyer, Mitth. a. d. zool. Stat. zu Neapel, 1887, Bd. VII, p. 203.

Inhibition (Voy. également : *Nerfs craniens, Pneumogastrique*).—Cl. Bernard, Vasodilatation, *Journ. de l'anat. et de la phys.*, 1858.—Brodie et Russell, Réflex. card. inhib., *Journ. of Phys.*, 1900–1, p. 92.—Brown-Séquard, Champ de l'inhibition, *Dictionnaire de Dechambre* ; Ac. carb. inhib. de la sensibilité, *Arch. Phys.*, 1891, p. 645.—Budge, *Arch. de Roser et Wunderlich*, 1846.—Gad et Orchansky, *Arch. f. Phys.*, Leipzig, 1887.—Gaskell, Variation électrique positive, *Journ. of Phys.*, 1887.—Gley, Inhibition sécrétoire, *Arch. Phys.*, 1889, p. 151.—Th. Hough, *Journ. of Phys.*, 1895, p. 161, vol. XVIII, p. 161.—Goltz, Herzund Vagus, *Arch. f. Anat. und phys.*, 1863 et 1864.—

Heidenhain et Bubnoff, *Arch. f. d. ges. Phys.*, 1881, Bd. XXVI.—Hering et Sherrington, *Arch. f. d. ges. Phys.*, Bd. LXVIII, p. 222.—Knoll, *Arch. f. d. ges. Phys.*, Bd. XLVII, p. 595.—E. Meyer, Inhib. vascul. chez le nouveau-né, *Arch. de phys.*, 1893.—Morat, Nerfs et centres inhibiteurs, *Arch. de phys.*, 1894 ; L'inhibition dans ses rapports avec la température, *Arch. de phys.*, 1893.—W. Mills, Hearth of Fish. *Journ. of Phys.*, 1886, p. 81.—H. Munck, Erregung und Hemmung, *Arch. f. Anat. und Phys.*, 1881, p. 553.—Oddi, Cerveau et moelle centres inhib., *Arch. it. biol.*, 1895, t. XXIV, p. 360.—E. Meyer, Inhib. vascul. nouveau-né, *Arch. Phys.*, 1893.—Is. Ott, *Journ. of Phys.*, 1880–82, vol. III, p. 163.—Pflüger, Ub. d. hemmungsnerv. Syst., Berlin, 1857 ; Fonct. des nerfs splanchniques, Berlin, 1855 ; *Canstatt's Jahresb.*, 1856 ; *Biol.*, 1857.—Schiff, *Arch. f. phys. Heilkunde*, 1849, t. VIII, p. 179.—Sherrington, *Proceed. Roy. Soc.*, 1893 ; *Journ. of Phys.*, 1894 ; Decerebrat. rigidity, *Journ. of Phys.*, 1898, vol. XXII.—Max Verworn, *Arch. f. Anat. und Phys.*, 1900, suppl., p. 105.—E.-H. et Ed. Weber in Handwörterb. d. Physiol. de Wagner, 1846 ; *Arch. d'anat. gén. et de phys.*, Paris, 1846, p. 9 ; Ann. Universali di Medicina del dott. Omodei, t. LXVI, p. 227.—Mac William, Mammal. Heart. *Journ. of Phys.*, 1888, vol. IX, p. 345 ; *Journ. of Phys.*, 1885.—Wertheimer, Inhibit. réflexe du tonus de l'estomac, *Arch. de phys.*, 1892.

Inhibition in the Invertebrata.—Phisalix, Centres inhibitoires des taches pigmentaires des céphalopodes, *Arch. Phys.*, 1894, p. 92.—Piotrowski, Muscle-nerve Physiol. of the Crayfisch, *Journ. of Phys.*, 1893, p. 163.

Shock.—Bastian, *Med. chir. Trans.*, London, 1891.—Bethe, *Arch. f. d. ges. Phys.* Bd. LXVIII.—Bruns, *Neurol. Centralbl.*, 1893.—Contejean, *Arch. Phys.*, 1894, p. 643,—Fr.-Franck, *Biol.*, 1877 ; *Trav. lab. Marey*, 1877.—Loeb, *Arch. f. d. ges. Phys.*, 1894. Bd. LVI.—Marshall-Hall, Synopsis of the Diastaltic Nervous System, London, 1850.—W.-W. Norman, *Arch. f. d. ges. Phys.*, 1897, Bd. LXVII.—Piéchaud, Thèse de Paris.—Roger, *Arch. Phys.*, 1893, p. 57, 601, 177 ; et 1894, p. 783.—Sherrington, *Phil. Trans.*, London, 1897.

Stoppage of the Exchanges.—Brown-Séquard, *C. R. Acad. sc.*, 1882, t. XCIV, p. 491 ; *Arch. de phys.*, 1891, p. 818.

Trophic Nerves.—Cl. Bernard, *Biol.*, 1873.—Bichat, Rech. sur la vie et la mort. Paris, 1829, 5e édit., p. 506.—Bidder, *Centralbl. f. d. med. Wiss*, 1874.—B. Brodie, cité par Brown-Séquard, *Journ. de la phys. homme et anim.*, 1859, p. 114.—Charcot, Leçons sur les maladies du syst. nerv., 1872–1873, p. 133.—Couyba, Thèse de Paris, 1871.—Duplay et Morat. Mal perforant plantaire, *Arch. gén. de méd.*, 1873.—H. Frémy, Trophonévrose, Thèse de Paris, 1872.—Knoll, *Sitz. d. k. Acad. Wiss.*, Wien, 1893.—Le Lande, Aplasie lamineuse, Thèse de Paris, 1870.—Legros, Des vaso-moteurs, Thèse ag. Paris, 1873.—Longet, Traité de physiol., 3e édit, t. III, p. 539.—Magendie, *Journ. de phys. exp.*, 1824.—Marinesco, *Neurol. Centralbl.*, 1898.—G. Meissner, *Gaz. hebd.*, 1867.—Obolensky *Gaz. hebd.*, 1868, p. 590.—Ollier, *Journ. de la phys. homme et anim.*, 1863, t. VI, p. 107.—Samuel, Die trophischen Nerven, Leipzig, 1860.—Schiff, *Biol.*, 1854, *Gaz. hebd.*, 1857.—Sherrington, *Proceed. Roy. Soc.*, 1896.—Stirling, *Journ. Anat. and Phys.*, 1876, vol. X, p. 511.—Vulpian, Leçons sur l'app. vaso-moteur, t. II.—Warington, *Journ. of Phys.*, 1897.

CHAPTER III

THE CONSCIOUS AND THE UNCONSCIOUS: THEIR SEPARATION

We have seen that the nervous system is, in a sense, divided into two portions, which we call *sensory* and *motor*, the characters of which have been pointed out. From another point of view it is divided into two great systematizations which are founded on another opposition, that which exists between the *conscious* and the *unconscious* nature of certain acts or functions which it performs. This opposition is no more absolute than is that observed between sensation and motion; but it seems to us to be so on account of the highly marked distinction which exists between the different states of consciousness.

The degrees of consciousness.—There is an *obscure* consciousness of being which does not analyse either the forms or the movements or the causes of these movements: this is never absent from our organs so long as they are attached to the nervous system as a whole, and we may conclude that it exists to some extent in the separate cellular elements; it is a form of unconsciousness, which is practically only subconsciousness. There is a *definite* consciousness of being which is sharply defined from that which surrounds it, and furnishes it with the forms, the qualities and the movements which come in relation with it from the external world; this is the perception of the ego, consciousness properly so called.

1. **Separation at the periphery.**—It is remarkable that the most definite consciousness arises from the most sharply accentuated opposition between that which is internal to us and that which is external to us; namely, of the excitations from the surface of our bodies (organs of sense) reverberating on muscles capable of reacting against the causes of these excitations; while our own organs, in exchanging between themselves excitations and reactions by the intermediation of the nervous system, only furnish us with sensations which are obscure, without precision, indefinite, incapable of analysis. The sensory nerves which start from the surface, the motor nerves which return to the superficial muscles, these are concerned with the cycle of con-

sciousness. The sensitivo-motor elements embedded in the depths of the body, these are related to unconsciousness. Anatomically speaking, the separation is here very definite; on the one hand a *somatic* system, on the other a *splanchnic* system whose characters will be analysed farther on.

2. **Separation in the cerebral cortex.**—Everywhere else the separation is much more difficult to make. Distinct sensation, the conscious phenomenon, is only developed as regards a cycle which includes the cerebral cortex. But the converse is not true, although it is often affirmed to be so. Certain cycles which are completed in the cortex do not end in a conscious sensation in the ordinary sense of the word. This is due to the greater or less extension which the excitation effects in the cortex, and to the facility of penetration which is here offered to it, according to the point of departure and the intensity of excitation. Those excitations which come from the senses have easy access to it, those coming from the internal organs a difficult one; but it is a question of degree.

3. **Separation between the deep and the peripheral systems.**—On the other hand, the excitation which has penetrated into the nervous system, especially in the cortex, is provided with means of remaining there when the communications with the organs of the senses are broken. The cycle of excitation is then split up in the direction of its elevation, into a superior *cerebral* cycle and an inferior *medullary* cycle, which are capable of independent functional action. Hence results a new division between the conscious and the unconscious: consciousness continues attached to the brain in the form of souvenir or remembrance of the anterior sensation; unconsciousness is situated in the inferior cycle which, in spite of its persistent relations with the organs of sense and the muscles, is reduced to the condition of a reflex phenomenon.

Variability of the limits.—Consciousness is not then attached to a rigid and permanent system of nerves, and still less to a special kind of cellular element. It takes its rise in the associations which, according to the requirements, are organized in the nervous system, and its degree becomes more elevated according to the complexity and the special value of these associations. More uniform, more automatic are those of the visceral functions; while the somatic functions are more contingent, more varied, and more complex, and hence it is that their value is so unequal from the point of view of consciousness.

In the analytical study which follows and passes in review the principal localities in which nervous associations are organized, we shall always bear in mind this double separation between sensibility

and motricity, between the conscious and the unconscious. It is at the foundation of nervous organization. It will guide us constantly in the study which we shall proceed to make of the latter as a whole, before describing the different modalities or special functions which introduce into it, in their turn, numerous subdivisions.

The problem of the conscious, its difficulties; current hypothesis.—Both naturally and by definition, consciousness is a phenomenon which we only directly perceive in ourselves The first classification which occurs to us is a distinction between our being and that which surrounds it. The *ego* is opposed to the *non-ego*. The *ego*, which is conscious of its being, and which sees beings outside its consciousness, willingly attributes to them unconsciousness, by opposition to that which it feels to be itself.

The conscious and unconscious apart from ourselves.—It is true that this delusion is somewhat rapidly rectified when it is a question of beings situated outside ourselves which narrowly resemble us in their external characters, as human beings; or which have considerable analogy with us, as animals. By indirect procedures, we thus recognize the existence of consciousness other than our own. On the other hand, the delusion is more enduring in proportion as we are removed from these special cases. At the first glance, it does not seem that consciousness can exist except under the form and in the degree which we recognize in ourselves. It may be asked, however, if consciousness is not a fundamental attribute of the being, an attribute whose complicated and very differentiated form in ourselves hinders us from recognizing its original and general nature. This manner of viewing the question is supported by the contemporary progress of biology. In proportion as, starting from ourselves, we are better acquainted with the filiation which attaches us to other beings, so much is the field of consciousness in nature enlarged. There only where the chain seems to us broken, at the line of separation between the organic and inorganic, does this field itself seem to terminate. But continuity may one day be found to exist where, at present, we see only discontinuity. However this may be, by remaining on biological territory, as it is at present defined, it may be said that, outside ourselves, the division between the conscious and the unconscious is not made in accordance with a distinctly traced line, but follows a zone progressively degenerating without determinate limits.

The conscious and the unconscious in ourselves.—In our own proper being there is a division between the conscious and the unconscious. The *ego* does not always occupy the whole of the organism, and it does not always occupy the same field in the latter. All that remains apart from the conscious field we call *unconscious*. But the same problem presents itself here as higher up.

Is this unconsciousness which is present in us an unconsciousness in the absolute sense of the word, or rather is it a consciousness which is limited to what is outside the *ego?* If we notice that the nervous mechanisms which record these so-called unconscious functions are (although of less elaborate nature) built up on the same plan as those which take part in conscious functions, we must admit that the second supposition is the more probable one. *The animal organism may be regarded as an association of conscious units of unequal value, and in which one of these units has assumed the directive action* (Durand de Gros).

Animal colonies.—Phylogenetic development seems to support this conception. As is well known, the invertebrata are composed of segments (zoonites), each one representing in miniature the organization of the animal to which they belong. Isolated the one from the other, they are yet susceptible of vital manifestations presenting a certain independence (Dugès).

In the vertebrata, the zoonites have become the *metameres* and have, fundamentally, the same signification. Metamerisation, at first clearly obvious in the embryo, is in the process of development reduced to a mere trace, and thus gives place to a very definite centralization in superior animals, especially in man. The vertebrata, according to this hypothesis, would not be the less an *animal colony* (E. Perrier), in which one of the conscious units (that which we call the *ego*) has taken the control of the whole and has reduced the other units to the condition of conscious servants having no initiative, servants so eclipsed that it ignores the initial filiation by which they are united to it.

Difficulties of the analysis of the phenomena of consciousness.—There would be then in the living being an organization of consciousness, just as there is an organization of force and of matter, and it is this very organization whose chief outlines would be rendered visible by the form and the structure of animals. These are simple indications reduced to a vague and indefinite condition. When analysis endeavours to penetrate into this domain, inextricable difficulties are encountered. Consciousness is the most imperceptible and the most mobile phenomenon which it is possible to study. We know that it is susceptible of augmentation, of reduction, of disintegration, of synthesis. Its field of action varies at every moment, absorbs neighbouring fields, or is detached from them, undergoes degradations, and passes, according to circumstances, into the subconscious, the unconscious, or the extra-conscious. Consciousness is like the living being in a condition of perpetual renewal, of perpetual genesis.

A. DISPERSION AND REFLECTION OF IMPULSES: THE SPINAL CORD.

The nerve roots are only conductors of the impulse. In the spinal cord these conductors are associated: through its grey matter it becomes an *apparatus for the transformation of the impulse* and, therefore, *for the organization of the nervous functions*.

The grey matter wherever it occurs is, if we may call it so, the keystone of the systems by which these functions are carried out. By it the connexions between the neurons are effected, the neurons being those which make up these connexions and contain the breaks which, at other times, dissociate them in order to substitute them reciprocally. From this point of view the functions of the spinal cord have for long been divided into two groups: the one including those which are perfected in inferior and very simple systems, organized in it, and which suffice for the performance of very simple functions (*reflex systems and functions*); the other including those in which these inferior systems, dissociating, yield up their elements for the constitution of much larger systems (*conscious voluntary systems and functions*).

They are distinguished by the fact that, in the first case, the spinal cord acts as a *centre of reflection*, and in the second as an *organ of transmission*. The two varieties do not differ fundamentally, for both imply the reflection and transformation of the impulse in the grey matter. The difference consists rather in that, in the first case, reflection occurs *towards the exterior*, in a manner which is both *direct* and *total*; while, in the second, it is effected *towards the depths of the nervous*

system, in which the impulse *is dispersed*, undergoing multiple and graduated reflections and transformations which generally *absorb* it in great part.

The word "spinal cord," in the sense in which it is used in descriptive anatomy, does not imply an organ having natural limits, but has merely the value of a topographical expression. In order to isolate this so-called organ, the scalpel of the anatomist separates the conducting fibres, some of which attach it to the brain (deep neurons or those of the second order), and others to the non-nervous organs (peripheral neurons or those of the first order). These neurons are connected amongst themselves in the spinal cord itself, as also with other neurons which are special to it. The limits of the elements and of the systems formed by the associations of these elements are, on the contrary, situated in the grey matter. This latter is therefore, by definition, a place of organization for nervous functions. In order to reach it, the conductors of the first and of the second order (peripheral and encephalic) both run a certain course in the white medullary tracts, where, completely isolated from the point of view of conduction, they are more or less intimately mixed.

An analytical study of the functions of the spinal cord must therefore be commenced by the recognition of these different elements, by seeking to isolate them functionally the one from the other, by ascertaining their properties with the help of localized stimuli, or by equally localized mutilations, so that an opinion may be formed concerning their function, either by its artificial excitation or by its deficit. The leading type of these experiments is displayed in those which have been performed on the roots, with this qualification, however, that the object under investigation has become much more complex, and that the experimental difficulties are therefore so much the greater.

1. Sensation in the Spinal Cord

It is necessary to consider apart the results furnished by local stimulations and those due to interruptions or equally localized sections of the medullary tracts.

A. **Stimulation of the grey matter.**—It has for long been maintained by physiologists, as a kind of dogma, that the grey matter is wholly inexcitable by irritants applied experimentally (electricity, pricking, chemical action, etc.). Chauveau had, however, proved that electrical excitation, applied to the floor of the fourth ventricle, threw into activity the nuclei of the motor nerves which take origin therein. The erroneous idea which was held concerning this matter was not wholly corrected until about 1870, by the work of Fritsh and Hitzig on the stimulation of the cerebral cortex. So far as concerns the spinal cord, Vitzou, operating on the inferior ventricle (*rhomboidal sinus*) of the spinal cord of birds, has shown that its grey matter can be directly excited by mechanical agents.

1. **Excitation of the centres.**—It is now common knowledge that, by stimulating certain regions of the grey matter, it is possible to elicit the motor properties of the motor nerves which take their origin in

them: this is what is called the excitation of the *centres* of origin of these nerves. Nevertheless, it seems that some confusion still exists concerning what should be called the excitation of a centre. This confusion arises from the fact that an inaccurate and indefinite idea is held concerning the organization and the functions of the centres.

Erroneous comparison.—Applied to a nervous conductor, the stimulus causes the manifestation of the function of this conductor; applied to a centre, it is maintained that it should arouse the much more complex functions of this centre, and make them appear in their normal order. But it is here that the error lies: the comparison is inaccurate. There is a tendency to forget that, in the first case, the stimulus affects a simple (or relatively simple) object, which has but one mode of response, by allowing it to pass into the sensory or motor organs, with which it is connected; in the second case, the stimulus is applied to an association, a complex arrangement of elements, all of which it affects at the same time, without regard to the special order according to which they should transmit this impulse in order to ensure its regular and harmonious effect. It is as if, in a piece of clockwork, the impulse were communicated to all the wheels at the same time, without any regard being paid to the direction or to the rate of their rotation; the mean effect of this would be a movement, but one not necessarily suggesting that which arises regularly when the apparatus is controlled by its balance wheel.

Simultaneous excitation of elements arranged in succession.—Of whatever nature may be the stimulus made use of, electricity, mechanical irritation (and electricity is almost the only efficacious excitant), it will reach simultaneously in the grey matter (in that which we call the centres) all the elements of which it is composed, whether these elements be sensory, motor, inhibitory, co-ordinating, associating, etc., it will place them in irregular conflict the one with the other, and will give the predominance to some of them, preferably to those which take origin in the centre, in such a way that the stimulation of the latter amounts to much the same thing as that of its motor or inhibitory nerves in unfavourable conditions. The only legitimate and regular means which we possess of causing the penetration of the stimulus into such a complex arrangement is to excite one of the nerves or, if we are able, one of the elements which come to it and whose proper function it is to arouse it to action in a definite manner.

It should be added, however, that, when the so-called centre has a certain longitudinal or superficial extent (like the spinal cord or the brain), the stimulus may be propagated from the locality directly

excited, according to its normal laws, to other portions, in such a way as to arouse the regular play of the system. This mode of stimulation may be made use of in order to analyse the system under consideration. It is not contrary to the rule which we have just formulated, of which it forms a particular case.

2. **Determination of reflex centres.**—This is what physiologists have clearly understood, so far as it concerns the centres of the reflex actions which are of the nature of those arranged in series throughout the length of the spinal cord and the medulla oblongata. *The action of such centres is defined by the comparison of the effects produced by stimulation of the centripetal and the centrifugal nerves.* The excitation of the centres has become important only when the brain has been studied. Here it is a question of surfaces or of areas rather than of centres. Stimulation of a portion of their surface amounts to the same thing as to cause the stimulus to penetrate this surface, in some definite locality, whence it is transmitted by physiological conduction to other portions. It may then manifest certain of the functional associations which are effected by the areas known as centres. These associations could not be manifested in their integrity; nor, especially, in their regular succession. It is necessary to be aware of this.

B. Stimulation of the Posterior Columns.—This has been effected in the frog, the rabbit, the dog and the large solipedia with more or less success.

1. **Total effect.**—The irritation of the posterior medullary columns by pricking causes *severe pain and violent reflex movements.* It thus acts in the same way as irritation of the posterior roots, and this is not surprising when it is remembered that the posterior columns of the spinal cord are in great part formed by the terminal prolongations of these roots themselves which follow in them both an ascending and descending course (this latter sometimes very long).

Endogenous and exogenous fibres.—But in spite of the preponderating position which the terminal expansions of the posterior roots (*exogenous* fibres) occupy in them, the posterior columns of the cord contain a certain number of special fibres (*endogenous* fibres). Taking origin in the grey matter of the posterior horns, they return thither, having formed between the different stages of this matter longitudinal commissures of relatively short length comparable to those which exist in the fundamental antero-lateral columns. These endogenous fibres present this remarkable feature that, after having received an impulse by their dendrites in the spongy substance, or the substance of Rolando, they redistribute it in two opposite directions, the one ascending, the other descending, by means of a bifurcation of their

axon, which sends one branch upwards and another downwards, both of which once again enter the grey matter of the spinal cord. The ascending branches form a tract which is situated in the anterior or ventral portions of the cord (*ventral tract, cornu-commissural zone, field of Westphal*) ; the descending branches form a tract which, according to the locality, whether dorsal, lumbar, or sacral in which it is investigated, assumes the aspect of a comma, of a tract, of an oval, or of a triangle.

Isolated excitation of the endogenous fibres.—What is the result of an excitation limited to the endogenous fibres, or those peculiar to the posterior column ? What is the function of these fibres ? But, first of all, what means is available for the separate stimulation of these fibres, to the exclusion of those of the posterior roots ? Physiologists have striven to discover such a means : (1) by experimenting in the interval between the roots, at a point as far removed as possible from the insertion of these roots, and by making use for this purpose of large animals (Chauveau) ; (2) by suppressing in a radical manner, by the supraganglionic section of the roots and the degeneration which is a consequence of it, the elements of these roots themselves up to their termination (Gianuzzi).

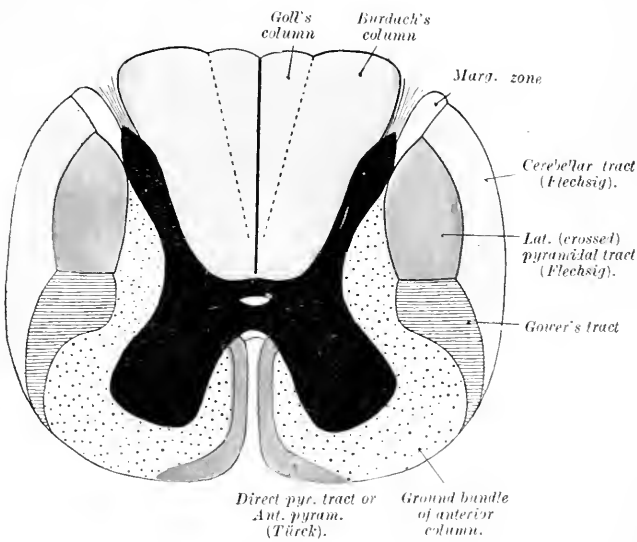


FIG. 109.—Tracts of the spinal cord.

Topography of the tracts in the cervical region. The pyramidal tract in red, the cerebellar in blue.

2. **Conclusion.**—The conclusion which must be drawn from these experiments is that *stimulation of the posterior columns, independently of the radicular elements which they contain, gives rise in the animal to manifestations of sensation, either painful or reflex.* This is the conclusion at which, with the exception of Van Deen, all investigators have arrived, with variations, it is true, in the results obtained. All are equally unanimous in maintaining that this sensation is less manifest than that which results from stimulation of the posterior roots.

Cl. Bernard, operating on the dog, finds the maximum sensitiveness behind, near to the median line ; Chauveau, experimenting on the

solipedia, finds it outside this locality in the neighbourhood of the posterior columns. These two investigators are unanimous in maintaining a great difference between the superficial (very sensitive) portion and the deep (almost insensitive) portion of the posterior columns

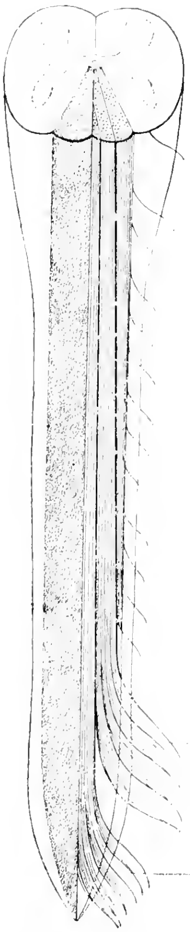


FIG. 110.—Structure of the column of Goll (Charpy).

Posterior aspect of the spinal cord On the left the column of Goll, shaded On the right the diagram shows that the column of Goll is formed by the long fibres of the posterior roots, and that in this column the fibres are more internal and posterior in proportion as they come from below.

All that has been furnished by anatomy since these observations on the constitution of these columns being taken into account, it is certain that these observers have acted most frequently on a mixture, in variable proportions, of endogenous and exogenous fibres, and the relative insensibility of certain regions is, according to them, the only criterion of the relative proportion of these two kinds of fibres the existence of which they were well acquainted with, but without knowing, as is now well known, their distribution. On the other hand, the experiments of Gianuzzi are extremely definite, they teach us that *after degeneration of exogenous fibres of radicular nature, there remain in the posterior columns special or endogenous fibres whose excitation still gives rise, in the absence of the first, to painful manifestations.*

Schiff, after having cut the posterior columns in a rabbit under the influence of ether, detaches them from the anterior portions of the spinal cord for a certain distance in the direction of the head of the animal. These columns thus detached, but still connected with the spinal cord, are subjected to stimulation (pinching) at their free extremity (as would be done on a sensory nerve); very obvious manifestations of pain are provoked, provided that the stimulus is not distant more than five or six vertebræ from the point where the columns rejoin the spinal cord.

This experiment should no longer receive the interpretation which was formerly given to it. Before the extremely oblique and prolonged course of the superior bifurcated branches of the radicular fibres in the columns of Burdach and of Goll was known, it seemed to be a proof at the same time of the existence and of the sensitive irritability of strictly endogenous fibres (the only ones considered to

run such a long course in the direction of the columns). It is now evident, on the contrary, that what are excited in the fasciculated bands thus separated from the grey matter for a considerable length are principally the ascending branches of the radicular fibres which have preserved their connexions with the grey matter at the upper portion of the tract thus separated. The endogenous fibres must therefore only participate to a slight degree in the production of the sensory phenomena elicited in this manner.

Ascending and descending sensory paths.—Following the example of Schiff, Brown-Séquard makes a section of the posterior column and detaches this column no longer above, but below the section (over a lesser length, it is true). The stimulation of this column also causes pain and reflex movements, still more intense, according to Brown-Séquard, than those which are elicited in the experiment of Schiff. It is a fact well established by a number of physiologists that an excitation, whether made above or below the section of the posterior columns, or of the entire spinal cord, with or without separation of the posterior columns finds paths both descending and ascending, by which it can proceed to the sensorium and give rise to conscious or unconscious reactions which prove the presence of sensibility. These descending paths, which had been unravelled by experiment, anatomy (which had formerly had a glimpse of them), now demonstrates in an obvious manner by means of its new methods; there are also *descending branches of the root fibres* as well as equally *descending branches of the endogenous fibres,* which disperse the impulse in the grey medullary matter, whether above or below its place of penetration, it the point of implantation of the dorsal root.

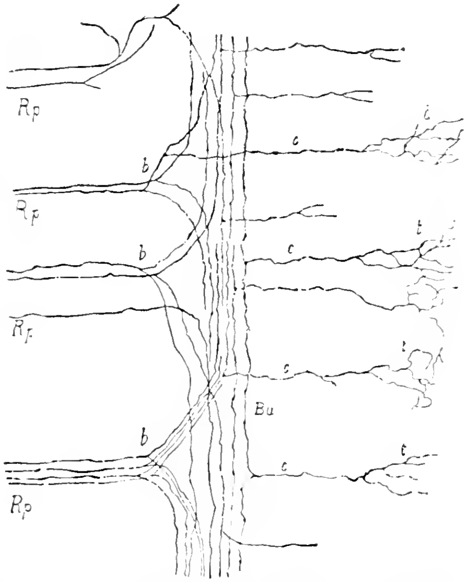


FIG. 111.—Collateral ramifications of the axis-cylinder prolongations. Sagittal longitudinal section of the spinal cord of a human embryo of 20 centimetres (after V. Lenhossék).

Rp, fibres of the posterior roots (central prolongations of the cells of the spinal ganglia): *b*, their bifurcation; *Bu*, longitudinal fibres of the column of Burdach; *c*, collaterals; *t*, terminal arborizations of the collaterals ending in the proximity of the cells of the grey medullary matter.

3. Direct and indirect prolongations of the sensory roots.—Thus the posterior columns are, on the one hand, the *direct* continuation of the posterior roots, of which they form the terminal prolongations scattered in the different regions of the grey medullary matter; and, on the other hand, the *indirect* continuation of these same roots after their interruption in the grey matter. In other words, they contain *elements of the first order*, the radicular neurons, and *elements of the second order*, the endogenous neurons, which receive the impulse from the first and enable it to pass over another stage. It is interesting to

know, by means of physiological experimentation, that the artificial stimulation of these neurons gives results which, if not identical, are at least of the same nature as those which are caused by stimulation of the posterior roots themselves.

Successive stages of the nerve cycle experimentally selected as point of departure of the excitation.—The nervous system is comparable to a mechanism whose components communicate movement the one to the other in a gradual manner and in a definite direction. Normally, the stimulus which acts upon it is received by the first of these portions, which is obviously constructed in such a manner as to be adapted for its reception. But if, artificially, it is communicated to it by the second or some more remote series in the mechanism, a motor effect is still possible, and this is what experiment clearly proves as regards the nervous system. Only, on account of the multiplicity of the transmissions and the variety of the movement, and of the complexity of the connexions, in proportion as the initial or motor component is departed from, the resulting effect loses its normal character, and this in any circumstances differs from that which results from the stimulus acting at the site of election. And this is easily understood if we remember that at each new transmission the connexions of the elements markedly change.

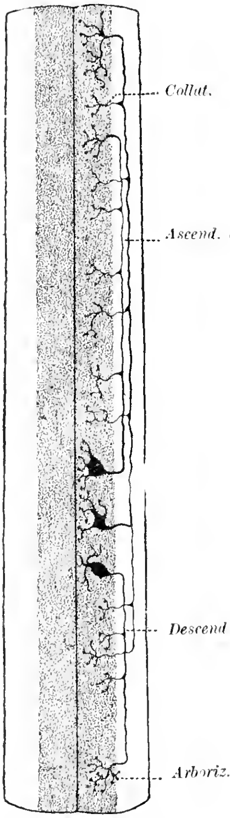


Fig. 112.—Cells of the spinal column.

Diagram showing the three types of the cells of the spinal column in longitudinal section, that of the middle portion being the ordinary type. The grey and white tints correspond to the two matters of the spinal cord.

Determination of the sensory field.—If we eliminate the nervous system as a whole and convey the impulsion to the muscles themselves or to their motor nerves, we still obtain movement; but a phenomenon which is altogether characteristic, and which accompanies it, has disappeared, namely, sensation. To ascertain what field the sensory phenomenon occupies in the nervous system, what systems employ it for the performance of their particular associated functions, is one of the problems with which we are confronted.

The experiments which precede solve this problem to a limited extent.

They prove to us that, *when deprived of its neurons of the first order, the nervous system when it is stimulated is still capable of sensation*, the field in which is continued the excitation provided artificially to the neurons of the second order, being still capable of permitting its development.

Difference of the effect according to the place chosen in the cycle.—But these same experiments show us also that the *sensory effect* due to these artificial excitations is *quantitatively less* than that which results from the stimulation of the sensory roots. And perhaps it is also *qualitatively different* from this latter, because, apart from the pain which is the common attribute of all sensory areas, it is impossible for us to ascertain in a certain manner if the excitation of the endogenous fibres of the posterior columns supplies to the animal any idea of tactile sensations properly so called, and any notion of position in space.

Paths of dispersion of the impulses in the sensory field.—The endogenous fibres of the posterior columns are indeed a continuation, not only *indirect*, but also *partial*, of the posterior roots. They only collect a portion of the stimulus which is distributed to the grey matter by the terminal ramifications of the posterior radicular neurons. The rest is collected by other fibres forming other columns which, in the spinal cord itself, build up formations parallel to the posterior columns. These are, in the lateral columns, *the column of Gowers and the direct cerebellar tract.*

Remark.—In the conditions which are imposed on experiment for the laying bare of the spinal cord and the preparation of its columns, it may indeed be asked if the sensibility which these columns manifest (even for their own fibres) is not quantitatively exaggerated, as happens in similar circumstances, for all parts artificially exposed. Experiment would thus deceive us concerning the real value of the phenomenon which it serves to render evident.

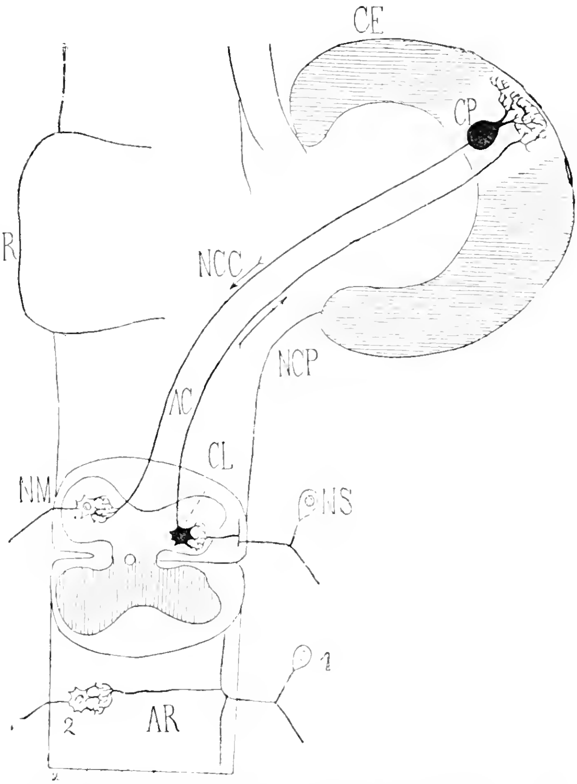


FIG. 113.—Ascending and descending cerebellar neurons (after M. Duval).

PR, pons; CE, cerebellar cortex: AC, reflex cerebellar arc; CL, cell of Clarke's column; CP, cell of Purkinje: NS, sensory nerve; NM, motor nerve; AR, reflex medullary arc.

Cerebellar tract—The cerebellar tract starts from Clarke's column and terminates in the cerebellum, in the grey matter of the *vermis superior.* Its ascending direction may be ascertained from the results of its degeneration. This tract conveys a certain portion of the tactile impulses towards this organ, whose function is still very enigmatical, and which, as regards the general consciousness of the individual, represents a special modification of consciousness necessary for the correct performance of certain movements or co-ordinated efforts.

Subserving more especially (as is shown by experiment) *the function of equilibrium,* the cerebellum co-ordinates and adjusts the movements by which this function is carried out; and it can only do this in pro-

portion as it is itself at every moment informed concerning the attitude of the parts, and of the changes in this attitude. It is easy to understand, as a consequence of this fact, that definite relationship between sensation and movement is present in it, as in the brain; but what especially distinguishes this relation from that in the brain we do not know, inasmuch as we have but little information concerning the exact nature and mechanism of the functions of both of these two organs. This tract would merit the appellation of *tract of Foville*, who was the first to ascertain its presence in the new-born infant, and has followed it up to the medulla oblongata and the cerebellum.

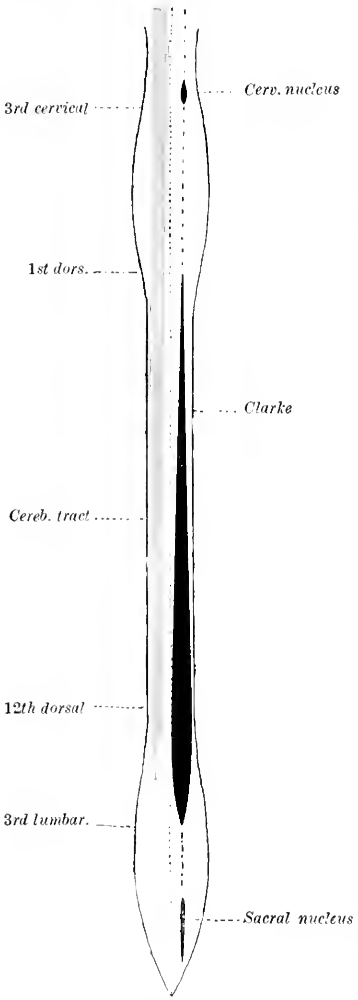


FIG. 114.—The column of Clarke and the direct cerebellar tract (after Charpy).

Relations as regards situation and size of Clarke's column (in black and on the right) with the cerebellar tract (in blue and on the left).

Tract of Gowers.—The ascending *antero-lateral* tract, called *tract of Gowers*, has another destination; it proceeds, at all events partially, to the cerebral cortex. Arising in the commissural cells of the posterior horn, its fibres pass from one side to the other, crossing one another; by following the anterior commissure, they then pursue a long course in the superficial and anterior part of the lateral column, reach the medulla oblongata, where they encounter a *nucleus of grey matter*, which partly interrupts them, and finally become united with the fillet or *ribbon of Reil* (lemniscus) running parallel to this tract, itself also of sensory origin, and thus reach the cerebral cortex. Concerning the origins of this tract in the spinal cord and its terminations in the encephalon, there are some differences of opinion amongst anatomists. The tract of Gowers sends, through the superior cerebellar peduncle, fibres to the *vermis superior* of the cerebellum. It has thus, partially, the distribution of the direct cerebellar tract.

Deep lateral tract and lateral ground bundle.—The remainder of the lateral column is occupied by two fasciculations, that of the *deep*

lateral tract, which touches the grey matter posteriorly, and that of the so-called *lateral ground bundle,* which occupies the remainder of the space. These fasciculations are formed of commissural fibres, which unite *en arc* the different stages of the grey medullary matter.

4. **Stimulation of the lateral column.**—Experiments have been performed on the lateral columns just as on the posterior and anterior columns. In order to understand the relation of these experiments, and at the same time that which they teach, it is necessary to remember that, for the most part, they date from an epoch anterior to that in which the sub-divisions of these different tracts into partial fasciculations, such as have just been pointed out, have been recognized through the study of myelination and of secondary degenerations.

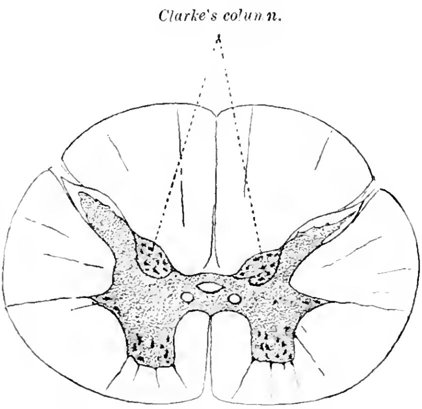


FIG. 115. Clarke's column (Charpy).

At the same time the three columns recognized by descriptive anatomy (anterior, lateral, posterior) were defined, but in reality only two of these were distinguished (the antero-lateral and the posterior). The sensory effects of stimulation are much less marked in the lateral than in the posterior column.

Since the first recognition of these details, new experiments naturally take into account recent advances of knowledge. As, on the other hand, the great difficulty is to experiment separately on tracts which are so closely approximated and sometimes mixed, an effort has been made to utilize the fact of the isolated and successive myelination of each of them, in order to investigate them separately on new-born animals in different stages of development. If, for example, a single tract is myelinated and the whole responds to the excitation, it follows that the resulting effect is dependent on this tract. If, on the other hand, a single tract is deprived of myelin and the result anticipated does not occur, it is because this result appertains to a non-myelinated tract (Bechterew). It is known that these tracts are excitable only when their fibres are provided with myelin, that is to say, when their development is complete.

Conscious effects.—The lateral column has therefore been completely severed, and its superior segment has been stimulated in the same way as the posterior column. A certain degree of sensibility has been found in it, but less than in the posterior column; this is explained by the absence, in the lateral column, of sensory radicular elements which (excepting in the experiment of Gianuzzi) have not been successfully dissociated from the endogenous elements in the posterior column. These endogenous elements thus manifest in a still more definite manner the weakness of their sensory effect.

Reflex effects.—The reflex effects of stimulation of the lateral columns are

like the conscious results, feebler than those aroused by the stimulation of the posterior columns in the neighbouring or corresponding regions. Yet these reflex effects are very definite so far as concerns the *cardio-vascular modifications*. Dittmar, who has studied them, observes that the centripetal stimulation of the lateral columns invariably produces them, while that of the anterior columns or that of the grey matter has not this effect.

According to Bechterew, hemisection of the cervical spinal cord is accompanied with movements of rotation and circus movements. If, further, the segment subjacent to the section in the region which corresponds to the direct cerebellar tract be irritated in the newly born dog, a movement of the trunk is elicited, the latter turning slightly on its axis, and of the head, which is inclined towards the shoulder of the same side. But at this period of development the cerebellar tract is completely myelinated, alongside of bundles which are not so, or are so to a very incomplete degree. The effects produced by the excitation would thus be due to the myelination. This tract would therefore be a conductor of the centripetal impressions which govern equilibration.

The antero-lateral tract, or that of Gowers, is only excitable in the dog, from the second or fourth day after birth. Its centripetal stimulation causes reflex movements of the trunk and of the thoracic limbs. As other centripetal paths, equally well developed, exist at that time in the same region, the conclusion to be drawn from this experiment is less precise. It may be maintained, nevertheless, with considerable probability that this tract forms an important sensory path.

C. Section of the Medullary Tracts.—Another method, applicable both to the spinal cord and nerves, consists in making limited sections of the grey axis of the cord, or of its tracts, in order to ascertain the *deficit* which results as regards certain functions, or the *conservation* of certain others. This double control should never be omitted in experiments on the nervous system.

1. **Hemisection of the spinal cord; conservation of sensibility in the corresponding portions.**—When made on one side only of the spinal cord, *section of the posterior columns does not abolish sensation in the part situated below this section.* This result was very surprising to the old experimenters, who regarded the spinal cord as being simply an assemblage of the peripheral nerves into a single trunk; it was, on the contrary, easily understood when the structure of this organ was unravelled, and more especially that of the posterior columns, and especially of the sensory roots, which in great part build them up. The field of distribution of each of these roots, and of each of the elements which compose them, is extremely large, thanks to the ramifications of those elements which are distributed both above and below in order to reach the grey medullary substance, in the greater portion of its extent. Section of the posterior column, above the lumbar enlargement for example, produces the same result as partial interruption of the connexions of the sensory nerves of the posterior limbs with the grey medullary axis. The impulses conveyed from the skin by the

posterior roots still continue to flow to it, by more limited paths it is true, but, nevertheless, they reach the sensorium. Ought it to be concluded from this that the route which is open to them in the complicated system consecutive to the radicular neurons is indeterminate, and that every path is available for them, provided only that it is permeable? Experiment does not confirm this, and such a supposition appears to be inadmissible from every point of view.

In the system which they help to form, each of the fasciculations, each of the elements which we consider separately, has its particular function, up to a certain specific point, which explains why if an element is destroyed or interrupted the system is no longer balanced, but is to a certain degree thrown out of equilibrium.

This is what seems to be the result of section of the posterior columns, with the exception that the modification produced by this section, as regards the exercise of sensation, is altogether unexpected.

Hyperæsthesia.—Fodera was the first to observe that, *after section of the posterior columns of the spinal cord, not only is sensation not abolished in the limbs situated below the point of section, but is on the contrary exaggerated.* This fact has since that time been re-examined by all investigators, and it is Brown-Séquard who has studied it in the greatest detail. According to this author, it is not merely sensibility to pain, but all modes of sensation (to heat, to cold, to pressure, to touch) which are thus increased. It may be truly said that, as a result of hyperæsthesia, these different modes of sensation are easily resolved into pain.

Reflex sensibility is also considerably exaggerated. Hyperæsthesia affects all the known forms of sensation.

Crossed anæsthesia.—Brown-Séquard has shown that, *if the section is made on one of the two posterior columns* the phenomenon of loss of balance of sensation assumes a new form: there is *hpyeræsthesia of the corresponding limb and hypoæsthesia,* that is to say, incomplete anæsthesia, *of the limb opposite to the side of section.* This is known as crossed anæsthesia.

According to Vulpian, there is a close connexion, a sort of balance, between these two phenomena, the one of exaggeration, the other of diminution of sensation.

Lesions varied as regards situation and extent.—In short, this phenomenon may be elicited by lesions which are varied both as regards magnitude and situation, but always on the condition that they are unilateral.

The most simple means, because it requires less precision, is to make a half section of the spinal cord above the origin of the nerves corresponding to the region whose sensation is being examined. The phenomenon still appears if *one of the lateral tracts* be cut in the region approximating the posterior column,

or if the posterior horn of one side be cut (Brown-Séquard). An extremely limited disorder of one side of the cord in the regions indicated suffices, a prick for example.

Persistence of the effects.—On the condition that the lesion produced persists, the phenomenon of the loss of balance and of sensation also persists for weeks or months ; in the case of irreparable lesion, it appears to be definite.

It may be equally produced by lesions situated, no longer in the thickness but in the height, of the spinal cord. If the hemisection is made in the cervical region, there is very marked hyperæsthesia of the two corresponding limbs and hypoæsthesia of the opposite side. If it is made near the medulla oblongata, there is in addition hyperæsthesia of the ear of the same side and hypoæsthesia of the opposite ear.

Action on the region situated immediately above.—Turck and Chauveau have observed, the first in the frog, the second in mammals, that an incomplete hemisection of the cord may equally cause hyperæsthesia of the parts situated in front of the lesion of the same side.

A hemisection of the restiform body, or of the anterior (superior) cerebellar peduncle, of the cerebellum, or of the corpora quadrigemina, causes a hyperæsthesia of all corresponding parts of the body, but only to a slight extent.

The reaction of the lesion is, as is obvious, very widespread as concerns the sensory regions situated behind (in man below) the hemisection. Whether the lesion be a complete hemisection or a destruction, very limited in thickness and height, or of the posterior column, the consequence of it reacts, not on any special limited cutaneous territory, but on all the sensory areas situated posteriorly, in an almost uniform manner.

2. **Explanation : decussation of the sensory paths.**—The crossed anæsthesia which follows hemisection of the spinal cord at first seemed to be very easily explained by an intercrossing of the conducting fibres, which was effected near to the point at which the posterior sensory roots enter the spinal cord. This opinion was held by Brown-Séquard, who supported it by the following observations :—

(*a*) On one side of the spinal cord (say the right) a hemisection is effected above the lumbar enlargement, and the anæsthesia of the opposite side crossed anæsthesia) which is the consequence of it is determined ; then hemisection of the cervical cord is made on the left side ; the consequence of this would be anæsthesia of the right anterior and posterior limbs, which had at first not merely preserved their sensibility, but were hyperæsthetic. The hemisection in both cases involves fibres which have decussated ; the dorsal those of the opposite portion of the superior limb only ; the cervical those of the anterior limb and of the posterior limb on the opposite side ; in this way the animal would have three limbs paralysed as regards sensation.

(*b*) The two halves of the lumbar enlargement of the spinal cord are separated by a longitudinal section : the consequence would be anæsthesia of the two posterior limbs, as if their sensory elements were involved at their point of decussation.

(*c*) The two halves of the cervical enlargement are separated by a longitudinal section ; the consequence would be anæsthesia of the two anterior limbs, but no lesion of sensation of the posterior limbs ; the section here would involve the site of decussation of the sensory elements of the anterior limb only, those of the posterior limbs having already decussated.

Restrictions.—These facts, as their author has since recognized, have neither the general application nor the precision which would be desirable if they are

to confirm the conclusion which in the first instance they had supported. The crossed anæsthesia which follows hemisections is not, it must be remembered, ever complete, and is sometimes little marked. In the bird, this hemisection is followed by anæsthesia of the same side. In the monkey, the anæsthesia produced by hemisection is particularly direct (Mott). In the frog, hemisection induces slight hyperæsthesia of the same side and no anæsthesia of the opposite side. Double hemisection, effected at different heights, permits the persistence of sensation in all the limbs; it merely diminishes it. Longitudinal separation of the two halves of the lumbar enlargement also merely produces a diminution of sensation in the two limbs.

Lastly, longitudinal section of the brachial enlargement does not exert an elective action on the anterior limbs, but merely produces an unequal effect on the four limbs, more markedly on the anterior, by destruction of the grey matter in this enlargement.

The following fact, due to Brown-Séquard, must be mentioned. In a rabbit a hemisection of the pons is made, for example, on the left: anæsthesia follows on the opposite side (on the right) and hyperæsthesia on the same side (on the left). Then a hemisection on the spinal cord is made on the right; inversion of the preceding phenomena results; the anæsthesia passes to the left and the hyperæsthesia to the right.

All these facts show that, as regards the development of sensation, the part played by the spinal cord is a very important one, but it is a part which at the present time can be in no sense defined. Amongst the explanations which must be rejected should be placed the one which regards the elements of the spinal cord as mere conductors transporting to the brain the impulse such as it has been received by the sensory nerves of the skin.

Partial and variable crossing.—The decussation of the sensory tracts, which was formerly supposed to take place immediately above the point at which the posterior roots join the cord, is then only partial at this spot. In certain species of animals it is very slight; however, the facts detailed above show that it is real, however limited it may be.

Anatomical Data.—The data subsequently supplied by anatomy are in complete accord with the results of these experiments. Amongst the tracts which from the grey axis proceed to the cerebral cortex, we observe at least one, the antero-lateral tract, or that of Gowers, whose fibres decussate near to its place of origin in Clarke's column and which then progresses in the half of the cord opposite to that in which it originated. Another crossing of the sensory elements, more important than the preceding, occurs in the medulla oblongata, in the immediate vicinity of that of the motor elements of the pyramidal tracts. The ascending branches of the radicular neurons, after having ascended in the posterior columns as far as the union of the spinal cord and of the medulla oblongata, while giving off in this course numerous collaterals in the grey medullary axis, exhaust their last ramifications in two nuclei (nuclei of Goll and of Burdach) which are the origins of a very important sensory tract, the fillet or lemniscus (ruban de Reil).

It is the fillet itself which decussates near to its origin ; shortly after its decussation, it joins on to the tract of Gowers, increases in size by the acquisition of the sensory elements coming from the bulbar nerves, and, thus constituted, proceeds towards the central convolutions of the cerebral cortex, not without presenting during its course an, at all events, partial relay in the optic thalamus.

Unilaterality or bilaterality of sensory representations.—The whole cutaneous surface of one side of the body should thus have, in a certain sense, its sensory representation in the cortex of the opposite hemisphere ; no doubt existed on this point until lately, and this view is generally maintained ; but the example of the sense of sight, in which the decussation is only partial ; that of the motor apparatus, in which the same side of the brain acts, although very unequally, on the muscles of both sides of the body, should lead to caution being exercised in this matter, and the more so because no means exists of absolutely controlling an entire and perfect decussation.

Galvanometric method.—The transmission of the impulse is accompanied, as is well known, by electro-motor phenomena (negative variation or current of action) which are rendered evident and are measured by the galvanometer. Gotsh and Horsley have observed that, on stimulating the sciatic nerve of one side, currents of this kind are developed in the lumbar segment of the spinal cord, these currents obivously accompanying the propagation of the impulse through this segment. But though these currents exist on both sides, yet they are always more intense on the side of the stimulation.

Syndrome of Brown-Séquard.—This name is given to a collection of symptoms consisting, as the result of *unilateral lesion of the spinal cord of motor paralysis of the one side combined with anæsthesia of the opposite side* (with or without hyperæsthesia on the side of the lesion). This association of symptoms recalls that which is experimentally effected by hemisection of the spinal cord. The combinations of anæsthesia and of hyperæsthesia may here also be very variously displayed.

3. **Medullary sensory paths of the deep organs.**—The evidences which are most often brought forward as a proof of sensory manifestations are the defensive reactions of animals which are performed by the muscles of the skeleton ; but certain movements of the deep organs, connected with the functions of organic life, may equally serve as very sensitive æsthesiometers. Miescher has performed experiments of this kind by registering the carotid pressure in a curarised rabbit, and by noting the variations which it undergoes as the result of stimulation of the sciatic nerve, both in the normal condition and when the spinal cord is incompletely divided, the section being performed above

the origins of this nerve. By making limited sections of the two lateral columns, and by proceeding to the point in which they meet in the thickness of the cord, the transmission of the impulse to the vaso-motor centres was almost entirely suppressed. Conversely, if the whole cord be divided, with the exception of one of the lateral columns, stimulation of the sciatic nerve on the opposite side caused the pressure to rise almost as much as in the normal animal; stimulation of the sciatic on the same side was nearly without result. The author has concluded that the site of the passage of the impulse thus made on the nerve of the inferior extremity is chiefly in the lateral column; that, further, this transmission is effected by paths, some of which are direct, but the majority crossed.

It must be remembered that the lateral column is formed of longer tracts situated more superficially, and of shorter or commissural tracts arranged longitudinally adjacent to the grey matter. In physiological researches it is at present necessary to give up the attempt to operate in a separate manner on these different fasciculations; as the difficulty of isolating the one from the other is very great, and still more so that of isolating the three fundamental columns of the cord which are visible to the naked eye from the grey matter.

In the anterior columns physiological experimentation does not enable us to recognize, any more than do the results furnished by anatomy, any element whose direction is ascending, in other words, a so-called sensory element.

4. **Important part played by the grey matter in the transmission of sensory impressions.**—A fact which has also been demonstrated by physiology, before anatomy proved it to be true, is the importance of the grey matter in the transmission of sensory impulses through the tissue of the spinal cord in order to reach the brain. That, individually, the posterior columns and a portion of the lateral columns take an obvious part in this transmission is easily understood from the experiments which have been described above; but, without the co-operation of the grey matter, it would be impossible for these structures to ensure the exercise of sensation. This is proved by the following experiment:

Experiment.—The whole thickness of the spinal cord is cut, with the exception of the posterior columns; sensation is abolished in the subjacent regions; even if, with the posterior columns the lateral columns are permitted to remain, when the rest of the cord is cut, sensation disappears. This is because the medullary grey matter plays a paramount part in the sensory functions and its section, by itself alone, completely annuls the functional activity of the tactile sensory system. This rôle would be demonstrated better and more clearly if it were possible to separately destroy the grey matter for a certain length, all the columns being left intact; but its central situation

prevents its isolated destruction. We are reduced to cutting it conjointly, sometimes with one column, sometimes with another. It is only observed (and investigators are unanimous on this point) *that an isolated section, or one combining that of the different columns, has no marked and complete anæsthetic action so long as the grey matter has not been divided throughout its thickness.*

This may be said at least as regards the sensation of *pain*, because some would make reserves concerning certain forms of sensation for which they consider that separate paths exist. More especially would tactile sensation have, in the posterior columns, its conducting fibres distinct from those which transmit painful impressions (Schiff), but the fact is disputed.

Situation of the grey matter intercalated in the course of the impulses.—When it is remembered that the grey substance of the spinal cord is the locality in which the radicular neurons, or those of the first order, come into contact with those of the second order, which conduct it towards the brain, and that it is hence a compulsory halting-place for the current of excitation which traverses the system of tactile sensation, the results furnished by experiment and the essential part which the latter attributes to it in the functions of this system will cause the less surprise. Doubtless the current of excitation follows the conducting fibres, both of the first and second order, but, to pass from one to the other, it cannot avoid the grey matter Every serious lesion of the latter may thus destroy sensation.

Paradox.—Yet it is difficult to explain, even with these data, how a transverse section of this grey matter, provided that it is complete, suffices to entirely abolish sensation in the regions posterior to it. It is surprising to observe that the interruption of this feltwork in one point has so decided an effect, resembling that of section of a band of parallel fibres. It is still more surprising to note that authors like Vulpian, who have studied this subject with the greatest attention and with scrupulous conscientiousness, affirm that a series of sections carried out in different directions, but incompletely, allows, on the contrary, sensation to persist; as if the impulses, which come from the posterior roots, could have in this grey matter an indeterminate course, an always possible means of flowing, on the one condition, that the continuity of the grey axis is not interrupted.

Lastly, and this is a no less astonishing fact, after these incomplete sections carried out in different directions, the animal still recognizes the site of the impression and turns to the side of the limb which is being irritated (Vulpian).

Remarks.—These facts suggest two remarks, already made by the authors of these experiments, and which it is advisable to refer to, namely: that experimental attempts to act in an isolated manner on such and such a portion of the spinal cord are extremely delicate and liable to error; and secondly, that the sensation displayed in these experiments is almost exclusively that of pain, and that the conditions of its production are more general and may be considered as less precise than those of other forms of sensibility.

2. Motility in the Spinal Cord

From the spinal cord proceed motor nerves which are distributed to most of the muscles of the body. These nerves represent the terminal

neurons of the tactile system; they convey to the muscles the impulse which they have themselves received in the spinal cord.

Multiple internal sources of motor excitation.—This excitation comes to them by somewhat varied routes, namely: (1) certain simple reflexes, directly from the sensory roots; (2) more complicated reflexes of the grey ganglionic nuclei arranged in series in the cord, the medulla and the base of the brain; (3) conscious voluntary acts of the cerebral cortex. It must not be forgotten that the common source of these stimuli is invariably in the sensory roots and the sensorial apparatus situated at their extremity. But this transmission, which is immediate and approximate for the execution of the reflex acts, is, on the contrary, mediate, and so much the more remote in proportion as it is a question of acts and of functions concerning instinct, and, above all, intelligence; the more these functions assume a psychical aspect, so much the longer is the duration of the impulse in the nervous system, the more complicated is the course which it runs in it, the more roundabout and prolonged are the paths, which, by compelling it to pass through the cortex, bring it back to the motor nuclei of the spinal cord.

Motor Field.—Just as, by comparison with the neurons of the posterior roots, those neurons are called *sensory* which proceed from the cord to the encephalon, so by comparison with the neurons of the anterior roots, those neurons are called *motor* which descend from the brain towards the spinal cord and the medulla oblongata.

That which distinguishes both of them from the strictly sensory and motor nerves is, as regards the first, that they no longer receive the impulse directly from the exterior; as regards the second, that they no longer directly transmit it to the organs of movement, but only by the obligatory intermediation of the nerves of the primary or inferior system. The first are nerves stimulated by nerves, and they react according to their nature and their organization; the second are nerves which stimulate nerves and equally make use of the organization of the latter, and no longer, like them, simply of muscular activity. The difference of the effects in the two cases results precisely from the transformations which take place in the transmission, from the fact of this organization whose existence they reveal to us, if not its internal details.

Cerebro-spinal motor tracts—Pyramidal tract.—Of these descending tracts the best known is that which forms the so-called *pyramidal* tract. It takes its origin in the central convolutions. Its fibres, mixed at first with those of the corona radiata, then proceed by the internal capsule, follow the crusta (pes) of the crus cerebri, pass through the pons varolii, partially decussate in the medulla oblongata, of which they form the so-called antero-pyramidal tract; the portion which does not decussate follows the anterior tract of the cord of the same side, while the decussated portion, which is much more important, accompanies the posterior portion of the lateral column, in which it forms a well-marked fasciculation. The *crossed pyramidal tract* extends to the fourth pair of sacral nerves; the *direct pyramidal tract* to the first lumbar (Dejerine and Thomas). Such is the arrangement in man.

In animals there is also a crossed pyramidal tract which accompanies the

lateral column of the cord, but the direct tract is not differentiated as it is in man, and does not proceed through the anterior column ; it is represented by fibres which follow the lateral column of the same side, being more or less mixed with the crossed fibres coming from the opposite side. In man an arrangement of this kind is sometimes present without interfering with the column of Türck which accompanies the anterior column. The decussation of the motor tracts undergoes very great variations according to the species, and even in different individuals of the same species.

Other descending paths.—Ground bundles.—In addition to these descending fibres of variable length, which form such a remarkable commissure between the cerebral cortex and the grey medullary axis, there are others which unite to the grey axis of the spinal cord either the ganglia of the base of the brain, or other parts of this axis itself. Like the ascending fibres, the descending cerebro-spinal fibres are of very variable length and form an infinite number of connexions, of which we clearly recognize only the most striking.

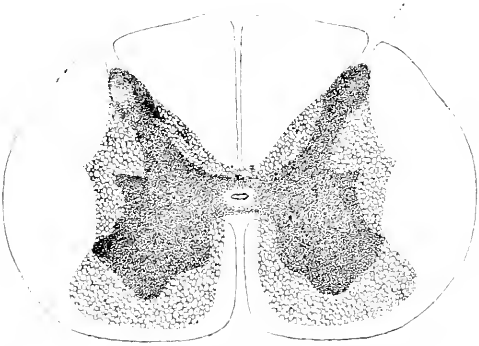


Fig. 116.—The short paths of the spinal cord.

They are grouped around the grey matter ; the white field corresponds to the middle or long paths.

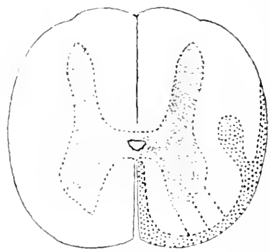


Fig. 117.—Descending cerebellar fibres.

Lumbar spinal cord : fibres of the column and anterior roots degenerated after extirpation of the cerebellum (Marchi).

The shortest commissural fibres are, as usual, those which directly approximate the grey matter, over which they are arched, like bridges of different lengths.

Yet further, an important formation in the ground bundle, the *posterior longitudinal* bundle, is to be noted, as it will be necessary to revert to it more than once.

Cerebello-spinal motor paths—Antero-pyramidal tract.—As is implied by its name, this tract is situated at the surface of the cord, at the periphery of the anterior and slightly of the lateral column.

As it descends it approaches the median line of the anterior fissure, which it soon skirts. The process of degeneration proves it to be a descending tract, formerly called motor (Lowenthal). It is a *centrifugal cerebellar* tract ; it degenerates after unilateral ablation of the cerebellum (Marchi) and after section of the inferior cerebellar peduncle (Basilewski). Helweg, Bechterew described yet another tract under the name of periolivary or olivary tract : it is a small superficially situated tract, which would connect the olivary body with the different stages of the grey medullary axis, and would be attached to the system of the cerebello-spinal connexions. The motor fibres taking origin in the cerebellum are not fixed in these more or less defined and recognizable formations, but are disseminated as far as the crossed pyramidal tract. These are those which are found to be degenerated in it after ablation of the cerebellum or sec-

tion of the inferior homolateral cerebellar peduncle. A tract called *intermediate* has also been defined.

The motor cerebello-spinal tracts are thus, as is obvious, the counterpart of the sensory spino-cerebellar tracts. Both provide between the cerebellum and the spinal cord a double current of impulses. The nervous cycle of which they form part thus supplies a particular form of the co-ordination of movements, *equilibration*. The elements of this cyclic system are, as will be seen further on, chiefly organized in the cerebellum.

1. **Stimulation of the descending tracts.**—The different tracts of the spinal cord have been stimulated in their normal condition, or after isolated section and separation of the neighbouring parts, in order to act upon them in the same way as upon ordinary nerves. In this way either the anterior or lateral tracts have been stimulated.

Preliminary question.—As regards all these descending tracts, from the very commencement of investigation, the same question has arisen as in the case of the ascending tracts.

How are the strictly motor elements of the spinal cord (the endogenous fibres) to be distinguished from the strictly radicular motor elements which arise in it from the anterior horns of the grey matter? Separate excitation of both is here much easier than in the case of the ascending elements. The field of origin of the motor radicular neuron has not, in the spinal cord, the same extension as the field of distribution of the sensory radicular neuron in its posterior portion. Instead of those bifurcations which, in the tracts of Goll and of Burdach follow such a wide course, the radicular neuron traverses the antero-lateral tract perpendicularly to its fibres, in such a manner that between the two anterior roots it is the special fibres of the spinal cord which are observed.

Apparent contradictions.—By stimulating the anterior columns in the interval between the roots, after or without previous section of the spinal cord or of these tracts, Longet has determined their excitability and their motor function. This result was then interpreted as implying a direct continuity between the columns and the anterior roots. Chauveau, on the contrary, experimenting on large animals, arrived at the conclusion that these columns *are inexcitable*. Like Longet, he makes use of electrical excitation; but, absorbed in avoiding its diffusion to the neighbouring motor roots, he graduates it carefully and maintains it at an intensity sufficient to stimulate the motor roots. He thus observes that the stimulus which arouses the functions of these latter does not produce any motor effect when it is applied to the columns in the interval between the roots. And this is the reason why he declines to admit the motor excitability of these columns.

2. **Decisive experiment.**—Vulpian has devised an experiment on

this disputed point which is decisive. In a rabbit or a dog, after it has been put under the influence of ether, he lays bare the spinal cord for a length of six to ten centimetres above its lumbar enlargement; he cuts all the roots which correspond to this length (in order that he may not have to take into account the movements which would result from their stimulation by the diffusion of the stimulating current). He cuts the cord in the most anterior portion of the region which has been laid bare and, throughout the extent of the latter, removes the posterior columns, a portion of the lateral columns, and as much as possible of the grey matter, in such a way that the anterior or antero-lateral columns (according to circumstances) thus separated are only connected with the cord by their posterior extremity. If the anterior extremity of the columns isolated in this way be pricked or compressed, somersaults are provoked; that is to say, contractions of the muscles of the hindquarters of the animal and movements of the tail. If, by following the anterior fissure, the two anterior columns be separated with exactitude the one from the other by a longitudinal incision, it is observed, by stimulating one of them, that much stronger movements ensue in the corresponding limb than in the limb of the opposite side.

In the newborn dog, the pyramidal tract is not yet myelinated. Stimulation of the lateral columns, when made at this period of development, does not produce the motor effects which ensue in the adult, or only from the epoch of the complete development of these parts (Bechterew).

Chiefly direct and partially crossed effects.—There is thus no doubt that stimulation of the anterior columns, and also that of the lateral columns, is followed by motor reactions attributable to this very stimulation. Further, this experiment shows us that the transmission of the impulse from these tracts to the motor nerves of the anterior roots is effected (in the grey medullary matter) chiefly on the corresponding side, and subordinately on the opposite side; in other words, that it is chiefly direct and very partially crossed.

3. **Quantitative difference.**—The experiments of Chauveau have nevertheless a very important bearing. If, indeed, we ought to modify the formula in which his conclusion is expressed and maintain with Vulpian and Longet the motor excitability of the antero-lateral columns of the spinal cord, we see from these same experiments (as also from that of Vulpian) that, *from the quantitative point of view, if not from the qualitative, there is a great difference in the excitability of the motor roots and of the antero-lateral columns*, and this proves to us that, if these two formations participate in the same general function, that of motricity, functional differences exist between them by which they

can be experimentally distinguished. In reality, these two formations are not the immediate prolongation, the one of the other, but are mutually connected by the grey matter, which, by establishing their connexions, transforms the current of excitation which passes through it.

Direct tract and crossed tract.—Stimulation of the anterior column is followed by undeniable motor results; that of the lateral columns is equally so. But these columns are complex formations and, further, they are not absolutely equivalent in man and in animals.

We leave on one side the ascending fibres which are present in the lateral column and which are excluded from the stimulation (as here practised) by the direction of their conduction. The anterior column contains the direct portion of the pyramidal tract, the lateral column contains that portion of it which has decussated in the bulbar pyramids. But, in both columns, to the tract known as the pyramidal another one is added, the ground bundle, formed of more or less lengthy commissural fibres which connect the superposed stages of the grey axis. At all events this is the arrangement in man; in animals the direct tract is almost completely wanting, and its elements are traced back to the lateral column of the same side. Experimental stimulation performed in animals, when it is applied to the anterior tract, thus chiefly affects the commissural fibres, and consequently renders evident their motor function; when it is applied to the lateral column, it affects, on the contrary, a collection of fibres in which the pyramidal tract occupies a prominent place from the motor point of view.

4. **Section of the antero-lateral columns.**—As the result of a large number of experiments made by different observers, it may be concluded that *section of the antero-lateral columns paralyses the movement of the subjacent muscles.* Thus it consequently interrupts the transmission of the impulses which descend from the superior regions of the nervous system, and only suffers the continuance of the most simple reflexes.

Section of the whole cord with the exception of the Antero-lateral Columns.—If, conversely, the whole cord with the exception of the antero-lateral columns be cut (for example, a little above the lumbar enlargement), movement is preserved in the subjacent members, and this is the counter proof of the preceding experiment, to the truth of which it bears witness. The movements which are thus preserved are not all capable of the same interpretation; some are *voluntary*, and proceed from the impulses starting in the cerebral cortex; others are *emotional*, and proceed from the optic thalamus; others, again, are *automatic*, and are the result of impulses originating in the mesence-

phalon. All the conductors, without doubt distinct, whose function it is to stimulate in the cord the elements which perform these movements, are contained in the antero-lateral columns ; the preceding experiments prove this.

5. **Part played by the grey matter in transmission of motor impulses.**—Section of the grey matter has not, as regards movement, the directly paralysing effect which is so evident in the case of sensation. It must not, however, be concluded from this that it plays no part in the transmission of motor impulses. Whether it is a question of motion or of sensation, it is always by the grey matter that the connexions are effected through which the neurons are joined together in a successive order ; the grey matter is a place of obligatory passage for the impulse transmitted from the one to the other. The difference, when the territories of articulation of the ascending and descending neurons in the spinal cord are compared, is that the first of these areas have a wide extension, while the second are gathered together and condensed in the very place which corresponds to the insertion of each motor root. From the experimental point of view, the consequence is that the first are encroached upon by every section which affects the grey medullary matter, while the second almost necessarily escape this section when it is made a little above the motor nerves which are the subject of investigation. But if the destruction of the grey matter occurs in this locality, it interrupts the communication between the cortical spinal elements and the radicular motor neurons, and a motor paralysis is the result.

Transformation of the impulse.—The grey matter of the anterior horns is not only a place of passage, but, as has been already remarked (Vulpian), *a place of transformation of the impulse.* The movements which are provoked by stimulation of the motor root are in no sense comparable to those which are caused by the stimulation of the pyramidal tract, from the cerebral cortex to the grey medullary matter itself. The first represent a crude effort of the muscles working altogether, without direction and without useful results ; the second represent, on the contrary, an ordered movement, one whose end is so much the more clearly defined in proportion as the stimulation affects a more restricted fasciculation in the thickness of the pyramidal tract.

Transported from the root nerve to the cortico-spinal nerve, the impulse assumes this new character : it is then that this last nerve is able to distribute it, or to cause it to be distributed, according to a definite order, to a group of neurons which make use of a muscular group with the view of the performance of a definite act. It is the organization of the motor function which is evident in this example

and which is effected by the connexion of the neurons in the grey matter.

6. **Direct and crossed action.**—It is known that the descending cortico-spinal fibres are crossed chiefly in the *bulbar pyramids.* When hemisection of the cord is effected, which necessarily interrupts these descending fibres on the side to which they are distributed, the corresponding limb is paralysed as regards voluntary movement, as was originally pointed out by Galen. Nevertheless, this paralysis is not absolutely complete, for, as we have already learnt by stimulation of the antero-lateral columns, a small portion of the fibres cross over in this same region from one side to the other. The preservation of the power of movement on the side of the hemisection varies in degree, according to the species, and also according to the conditions of the experiment.

In the frog, it is very obvious (Van Deen, Valentin, Stilling); in mammals, it is less marked, but can still be observed (Stilling, Brown-Séquard). The motor paralysis is the less marked in the corresponding limb in proportion as the hemisection is made more anteriorly as regards the motor organs under consideration. According to Vulpian, a hemisection made immediately in front of the nerves going to the posterior limb completely paralyses this member: if made in the cervical region, the anterior limb is then paralysed; but the corresponding posterior limb preserves its movements, as does that of the opposite side, which is also slightly weakened.

Syncineses.—For every movement in a determinate direction, such as flexion, extension, abduction, etc., of a limb or of its component segments, there is obviously an association of muscles, some co-operative, others antagonistic, whose resulting action determines the nature of the movement, together with its rate, strength and all its special circumstances. This association can only take place through the nervous system, and, in the latter, only by means of the grey matter. As regards certain of the most simple of these associations, it is clear that the grey medullary matter is by itself alone capable of performing them. If, indeed, the cord be cut in the dorsal region of a frog, and if some only slightly sensitive portion of the posterior limb be irritated, such as the extremity of the toes, so-called reflex movements, are provoked, which are co-ordinated movements; for example, a flexion of the different segments of the limb which thus avoids the stimulation; or, if the latter be stronger, it will be an abrupt extension of the two limbs of the animal, as if it were in flight (Vulpian).

These co-ordinated movements, performed by the cord separated from the medulla oblongata (and consequently separated from all the superior centres), have been noticed by a large number of observers: by themselves alone they render very improbable the opinion that the cord, in man, is deprived of all reflex power. Chauveau has remarked them in the solipedia, Brown-Séquard in the rabbit, Tarchanoff in the duck. In a horse or an ass whose cord has been cut below the medulla oblongata and in whom artificial respiration is performed, the reflex excitability of the cord is very great. If the pastern of the limb (opposite to that on which the animal is lying in order that it may have liberty of movement) be grasped, this limb is drawn back towards the trunk by abrupt

flexion, accompanied with some alternate movements of extension, sometimes indeed with an abrupt extension simulating a kick.

Co-ordination in the reflex system.—A duck, just decapitated and placed in a basin of water, performs regular natatory movements which are provoked either by the stimulation of the superior portion of the cord, or by that of the peripheral nerves.

In this case no other system of co-ordination can exist than the reflex system, and in the latter there is no other locality in which association of the elements can be effected save the grey matter of the lumbar enlargement. If, instead of stimulating a nerve coming from the skin, we stimulate one coming from the brain, we shall observe very similar or very analogous movements, which are invariably co-ordinated. In the one instance as in the other, the impulse communicated to a conducting fibre has fallen into a system adapted to impress upon it its direction, its succession, its relative intensity; in a word, the order best adapted for the attainment of the motor results. In the first case (reflex action), it comes from the skin, that is to say, directly from the exterior; in the second case (voluntary action), it comes from the cerebral cortex, that is to say, from another locality in which grey matter exists; or, expressed in yet another way, from a systematized whole infinitely more complex than those assemblages which are present in the cord. We thus see this superior system making use of simpler systems in order to carry out actions which it has itself prepared by the work of comparison, of co-ordination, of elaboration, to which it has submitted the impulse coming to it from the periphery, that is to say, from the exterior.

Convergence of the impulses in the motor field.—In both cases, an impression or an impulse is carried to a long distance. And this projection is made in the same apparatus, that is to say, in the same small aggregate of associated nerve elements. The casual or original difference is, however, extreme, since, in the first case, the stimulus is purely *mechanical*, while in the second it is *physical*, that is to say, bound to a sensory phenomenon which precedes and controls it.

Simple and complex systems.—By this analysis the systematization of the nervous tissue is made evident; I mean the association of its elements into systems at first very simple which, in their turn, are associated in succession or in juxtaposition, so that they form larger systems; and it is the same with these latter, so that the nervous system properly so called may be built up. Of whatever nature the system to which we turn our attention may be, whether simple or complicated, we shall find in it *internal bonds of union* which assure its continuance and also its functional individuality, and *external bonds of union*, which connect it to others in a larger system and one of different order.

Indeterminate limits; Changing constitution.—The greatest difficulty consists in tracing the exact limits of these associations and the exact order in which they are superposed and fitted together, because obviously these boundaries are not definitely determined or fixed in their situation. When the impulse arrives in a system and spreads through it, it seems to fade away at its boundaries by insensible diminution; it is resolved in order that with certain of its elements it may reproduce another impulse with the object of performing a different action. This is at least the case as regards especially the actions known as those of the life of relation with the exterior; the internal functions of the vegetative life are much more fixed and uniform, and their changes are, indeed, restricted to an obvious periodicity.

Method of association of the neurons.—Concerning the mode of association of nerve elements, in order that definite functional groups may be formed, anatomy has supplied some important information. These elements enter into relation and communicate the impulse which has put them in action by their ramified prolongations. The knowledge of these relationships, not merely in

general, but also in detail, would be of the highest interest, because it is clear that on the special disposition of these connexions the functional associations which we endeavour to ascertain depend. The little that is known on this point deserves to be recorded.

Overlapping of the Polar Fields.—*When two neurons transmit the impulse, the polar fields* (terminal of the one and initial of the other), greatly ramified, by which they come into relationship, *are not exclusively but only partially superposed*, while the remainder corresponds to portions of polar fields belonging to other neurons.

In this manner *a neuron transmits*, or can transmit, *the impulse to several others* (sometimes to a very large number), and distributes it thus in very diverse and remote regions: conversely, *a neuron receives the impulse from several others* (sometimes also from a very large number) and concentrates it in one point after having received it from multiple and distinct regions.

Examples.— The spinal cord supplies us with very characteristic examples of both arrangements. An element of a posterior root, taken by itself, distributes the impulse (by means of the grey matter) to radicular motor neurons, to the cerebellum, to the cerebellar cortex, to the optic thalamus, speaking only of the principal localities towards which it is distributed. An element of an anterior root, taken by itself, receives the impulse (by means of the grey matter) from posterior radicular neurons, from the cerebellum, the optic thalamus, the cerebral cortex, etc. (*see* Fig. 104).

Direct and derived transmission.— Another method of formulating the relationships in a more general and synthetic fashion is the following:—

When two neurons transmit the impulse to each other they generally do so in two ways, namely: (1) *directly by their own prolongations*: (2) *indirectly by neurons placed derivatively on these terminations.* These derived neurons, when they are short, are called associating neurons. As a matter of fact they are of all possible lengths. When we especially examine the connexion of the posterior and anterior radicular neurons of the cord we see them communicating the impulse, in addition to their direct prolongations, by means of the cerebellum, of the cortex, of the cerebral ganglia. Other paths of association, medium, short, very short, fill up the gaps left between these remote masses.

Elements of projection and elements of association.— To speak precisely, the so-called elements of projection are elements of association when they unite the nervous organs; two masses of grey matter, however remote the latter may be; for these elements have all possible dimensions.

Each segment of the spinal cord, even when regarded as separated from its neighbours by section, still contains, for its own special functional activity, these short cells of association, which doubtless take part in the most simple reflex actions arising in these segments. Further, the neighbouring or more or less remote segments are connected by elements of the same kind, whose length is progressively greater. These cells, known as co-ordinating or commissural, often present an arrangement which explains the redistribution which they impose on the impulse reaching them. Their dendrites are limited to the circumference of the cell; in other words, their receptive pole covers a limited field. Their axon, after running a short course, divides into two branches, the one usually ascending, the other descending in the columns, and sends collaterals to the grey matter to which they return; their distributive pole occupies a relatively very extended area.

The large commissures which connect the cord to the superior grey masses, when they arrive at the latter, obey in their turn the same law. The ascending and descending elements which compose them form direct connexions in these masses by articulation of the one with the other; but, further, they are second-

arily connected by elements of association or of derivation of diverse and extremely numerous categories, whence arises the very complicated structure of these organs.

Extra and intra-medullary distribution of the impulses by the same neuron.—It is owing to the advance in anatomical methods that it is now possible to say, from the inspection of a neuron, which are the points in it of entry and of exit of the impulse. The radicular motor neurons of the spinal cord receive the impulse by their dendrites (formerly known as protoplasmic prolongations); they transmit it by their axis cylinder or axon, which carries it to the muscles by these ramified terminations; but, before leaving the cord, this axis cylinder gives off, in its course through the anterior cornua, collateral branches, which, before leaving this organ, distribute in it a portion of the impulse to the elements which approximate them. It hence follows that the radicular muscles excite not only the muscles, but the motor neurons in their vicinity, which, in their turn, finally discharge the impulse received in the muscles; in other words, and conformably to the general law, they stimulate the muscles at the same time both directly and indirectly, and furnish a new example of this overlapping of the nerve elements the one over the other, which appears to be the fundamental rule presiding over their connexions.

Another example.—The neurons of the pyramidal tract offer an arrangement of the same kind which is still more definite. Their axis cylinder, near its origin, supplies collaterals of which certain very long ones would represent, at all events partially, the fibres of the corpus callosum, which functionally connect one hemisphere with the other; further, in the locality in which it passes through the pons, it supplies others not less remarkable on account of their situation, in the middle course of the axon which furnishes them, and which distribute the impulse to elements which proceed to the cerebellum by its middle peduncle.

Thus an impulse, even if supposed to be localized in the dendritic plume of a neuron of the pyramidal tract, has several paths open to it by which it can attain the motor nuclei of the spinal cord; the one direct, long known; the others indirect, by the opposite hemisphere, and by the cerebellum, without including other possible paths, all of which converge towards the anterior horns. And having arrived there, the same scheme is reproduced, but in a more restricted manner as regards the radicular neurons, which carry this impulse to the muscles directly by their terminations and indirectly by their collaterals. The nervous organization thus seems to have for its first and essential aim the multiplication as regards the impulse of the paths and conflicts, to drive it back from element to element, and to graduate its rate before recondensing it on the extreme terminations of the motor paths in order to impose on it an order, a definite succession adapted to the result to be obtained.

B. ANIMAL AND ORGANIC LIFE—THE GREAT SYMPATHETIC.

Anatomists, and with them many physiologists, divide the nervous system into two great secondary systems: the one known as the *cerebro-spinal system*, the other as the *great sympathetic system*, both recognizable by very obvious external characters. According to them, and following the ideas and expressions of Bichat, the first takes part in functions of the so-called *animal* life, or that of *relation*, the second in the functions of the *vegetative* life or that of *nutrition*. At the first glance these expressions, and the ideas which they formulate, appear to be very clear; experiment has not formally contradicted them; in

enforcing precision, it has gradually shown that they are too schematic and too absolute. Each of these terms, both from the anatomical and physiological point of view, ought to be defined; and it is by bringing these definitions in accord with the experimental data that the degree to which they have changed since the time of Bichat is recognized.

1. The two lives: their distinct representation in the nervous system

Are there then in reality two lives, the one animal the other vegetative? Is the animal life represented by a collection of organs possessing sensation, intelligence, motor power, grafted on a vegetable life represented by organs of nutrition, to such a degree that it is possible to ascertain and follow out, scalpel in hand, the manner in which one is fused to the other? No; Bichat's definition has only a figurative, an imaginary value. It is certainly very deep, but, from that very fact, it eludes a simple localization such as that pointed out above, which nevertheless has the great merit of being easily grasped on account of its simplicity. Aristotle had already observed that the functions of the living being may be divided into two orders: the one regarding more especially its conservation (vegetative functions or those of nutrition), the other concerning its connexions with the living world external to itself (social functions or those of relation). By re-

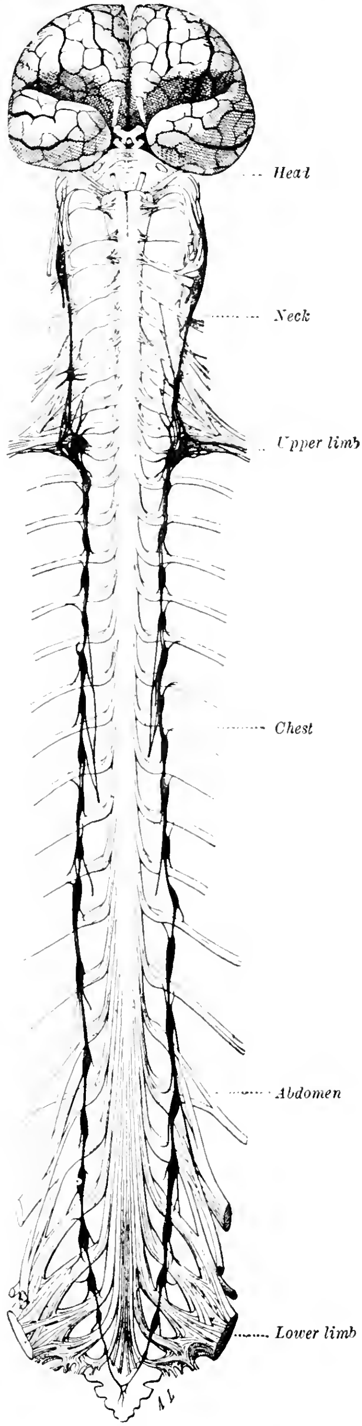


FIG. 118.—Deep nervous system.
The encephalon, the spinal cord, the great sympathetic.

garding the internal organs such as the heart, the lung, the intestine, it becomes obvious that they are intended for maintenance of life, for nutrition; on the other hand, the organs of sense, the apparatus of expression and of external movement, are adapted for the relationship of the animal with the medium which surrounds it, and especially with the living world. But the line of division is not fixed at the immediately visible organs. Every cell, every organized part, presents it once again in its more restricted area: in every cell indeed there is a portion of the protoplasm which is especially concerned with its maintenance and conservation, and another portion which discharges the social function with regard to other cells, bringing them into relation with itself.

And if ever analysis shall penetrate still farther into the organization of this complex being, the cell, the same division will apply to every differentiated portion of this miniature organism. In short, animal life and vegetative life are not two separate things, but two different aspects of the functions of the living organization, aspects which are encountered in every system of complicated organs when they are analysed. *Each group is united to analogous groups by external bonds of union, while its constituent parts are connected amongst themselves by bonds of union internal to the group itself.* The totality of the living kingdom is a system of this kind which analysis decomposes into smaller and smaller groups, until the elements of dead or of mineral nature are reached.

So-called Cerebro-spinal and Great Sympathetic Systems.—To return to the systems known as cerebro-spinal and great sympathetic; their reciprocal functions are, as a whole, those of relation (like every nervous function); only *the first established relations between the organism and the exterior, while the second forms relationships between the organs of the same organism*, indirectly for certain of these organisms, directly as regards those which exercise the conservative function known as that of nutrition. This much being said concerning their functions, how should these two systems be limited the one with regard to the other?

Signification attributed to these terms.—On this point, as also concerning the former, the ordinary meaning attributed to the terms *cerebro-spinal* and *great sympathetic* is illusory, because it is too absolute. Clearly distinct at the periphery, at the level of the differentiated organs between which they are distributed, these two systems form a single one in the superior portions of the nervous system, in order to ensure the unity of the latter and hence that of the organism. Although the anatomist, for reasons of convenience, traces a conventional line of demarcation between the two, this is merely a device,

certainly a useful one, but which must not cause us to lose sight of the reality.

The brain and the spinal cord enclosed in an osteo-fibrous cavity (the encephalo-spinal cavity) form an apparently homogeneous mass, which is invariably compact and known as *central*. Nerves arise from the spinal cord and by their prolongations form a feltwork of conducting fibres which are known as the *peripheral* nerves. This central mass, with its feltwork, is the cerebro-spinal system of anatomists.

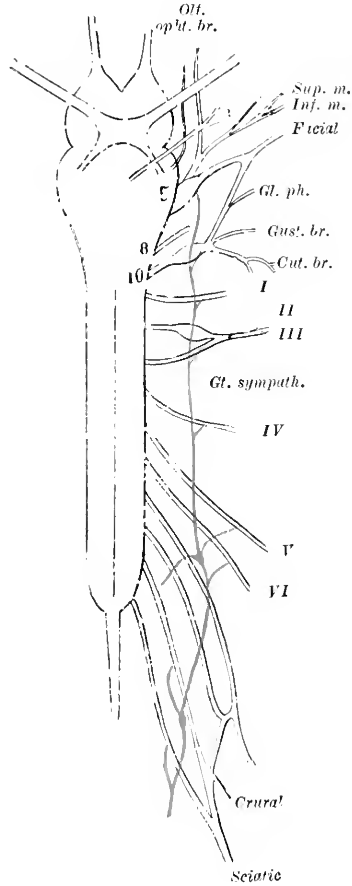


FIG. 119.—Encephalon, spinal cord, and great sympathetic in the frog. 3, oculo-motor; 4, pathetic; 5, trigeminal; 8, auditory; 10, pneumogastric.

On the other hand, nerve roots are seen, after leaving the spinal cord, to be detached from small bundles (communicating branches), projecting themselves into a double chain interrupted by ganglia, and from which cords arise forming a plexiform whole, itself being strewn with ganglia, which proceed to the pulmonary, digestive and vascular apparatus, that is to say, to the organs of nutrition: this is the great sympathetic system such as it is still described in all treatises.

Intra-rachidian prolongation of the Great Sympathetic System.—Experiment has convincingly shown that this second system communicates with the cord, and therefore with the brain itself, with which it effects an exchange of impulses. Thus the division of nerves into those of nutrition and those of exterior relation is inaccurate, and the terms which define it are deceptive; it gives a preference to the second to the detriment of the first. The cerebral and spinal mass is not, as is obvious, excluded from the control of nutrition, the great sympathetic is not the only one to safeguard the conservation of the organism. This has long been recognized, and has been for certain observers a reason why they deny all distinction between animal and nutritive functions and reject every systematization based on this distinction. This is to fall into the opposite mistake; it is to introduce

confusion once more into a subject which can be rendered clear only by persevering analytical efforts.

Of the theory of Bichat the most essential part must be retained, but its formula must be corrected in such a way as to make it agree with the facts of experiment. It is especially necessary to discard designations which are deceptive, or which have only an indefinite meaning. The system which physiology describes as that of " animal life " is not exactly that which anatomy calls " cerebro-spinal " ; its limits are less wide than this designation indicates, since the cord and the brain are also concerned in vegetative life and contribute to regulate it as well as that known as animal life. Conversely, the system which physiology calls " vegetative life " is not merely that which anatomy describes as " sympathetic," a term which, further, has no longer any meaning, the sympathies (a kind of functional consensus which the old physiology held to exist between remote organs) being assured as much by one of the two systems as by the other, and reciprocally.

In spite of this, the anatomical expressions currently used will still be employed, even by those who appreciate their inaccuracy or their insufficiency. We must therefore make use of them ; and this is the reason why it is necessary accurately to define the true meaning which attaches to them.

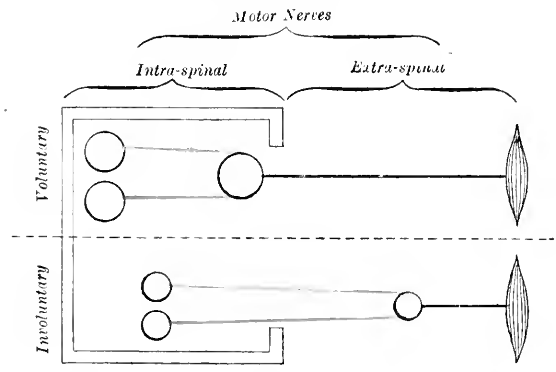


Fig. 120.—Diagram showing the anatomical characteristics of the motor systems, one being voluntary and the other involuntary.

As regards the first (called cerebro-spinal) the locality of union of the two orders of peripheral and deep neurons is intra-spinal ; as concerns the second (known as great sympathetic), it is extra-spinal.

Motor-nerves in black, excito-motor in blue, inhibitory in red.

Anatomical difference between the two systems.—From the point of view of descriptive anatomy, the difference which exists between the animal and the vegetative life is that the first has its grey matter, its centres, altogether contained in the cerebro-spinal cavity, while the second has a portion of this grey matter distributed outside this cavity. This extra-spinal grey matter, represented by the ganglia both of the chain and the plexiform cords of the second system, is precisely that which distinguishes the great sympathetic from all other nerves. *The great sympathetic is a sort of spinal cord, or a portion of the spinal cord, disseminated in the nutritive apparatus.* The chief nervous mechanisms, such as the reflexes, inhibition, summation of stimuli, etc., are recognized by experimental analysis, both in the metameric segments of the spinal cord and in the ganglia of the great sympathetic. The grey matter of the ganglia is further constructed histo-

logically, as regards its main outlines, in the same manner as the spinal cord and the brain; arborizations of neurons, some terminal, others initial, are intermixed and articulated in it as in the grey medullary axis and the cerebral cortex; and, further, the swollen bodies of these neurons find place in it in the midst of these arborizations.

The limits of the Great Sympathetic.—In accepting the great sympathetic as the extra-spinal portion of the nervous system of vegetative life, it is still necessary to define the limits which appertain to it, and on this point the confusion has been great. As has been mentioned, the great sympathetic is continuous with, and has the same origin as, the cord. But the latter comprises two portions, namely, the spinal cord and the medulla oblongata. The relations of the great sympathetic with the spinal cord should be taken as a type for the description because they are simple and symmetrically repeated throughout the length of the medullary cylinder. The relations of the sympathetic with the medulla oblongata, in which the typical form of the cord, properly so called, has disappeared, will only become clear by comparing them with the arrangement of this latter.

Its communicating branches.—From each mixed trunk resulting from the fusion of the anterior and posterior roots of a spinal nerve a small branch called *communicating* is detached, which proceeds to enter the chain of each of the great sympathetic at the level of each of its ganglia. Having arrived in the chain, the fibres of this branch ascend or descend through the length of the latter, following a variable course, before again leaving it, also at the level of one of its ganglia. The origins of the great sympathetic are situated both in the cord and the ganglia, including

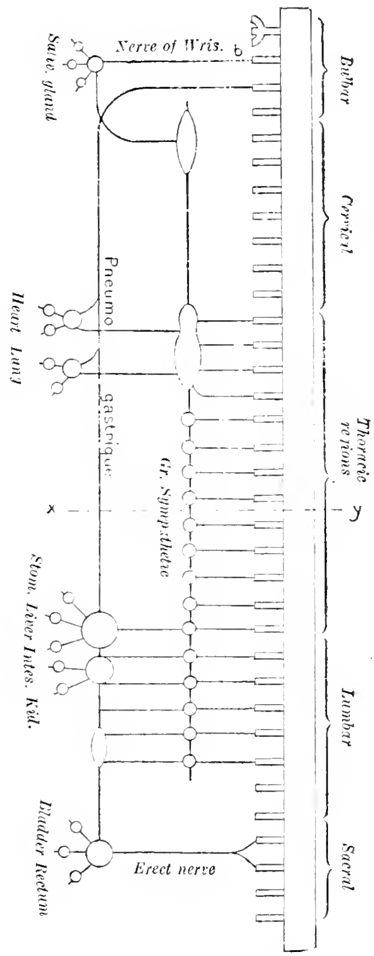


FIG. 121.—Diagram of the great sympathetic representing its visceral distribution.

On the right, medulla oblongata, spinal cord and roots. In the middle, vertebral chain and its ganglia. On the left, second chain (prevertebral), formed by the pneumogastric nerve and the mesenteric nerves, solar plexus, and hypogastric plexus. On the extreme left, terminal ganglia and plexuses of the viscera.

The break between peripheral and deep neurons is effected either in the catenary, terminal or intermediate ganglia.

Symmetrical with regard to a plane *xy* which intersects the thorax. Principal condensed origins in the thoracic region. Supplementary origins arising from the medulla oblongata (nerve of Wrisberg and pneumogastric) and from the sacral spinal cord (erector nerves).

those of the chain; by this is implied that the fibres coming from the spinal cord are, at least partially, interrupted in the chain. Thus from the chain branches are given off which, after having formed plexuses and passed through new ganglia, are distributed in the three great nutritive apparatus, *the digestive tube, the pulmonary apparatus, the vascular apparatus,* and also in the genital apparatus in its deep organs.

Its visceral and cutaneous branches.—As regards the organs which form clearly individualized masses, such as the intestine and its large glands, or the heart and the aorta, these branches extend directly from the chain to these organs; but as concerns those which, like the muscular and cutaneous vessels or the cutaneous glands, are disseminated interstitially in organs other than those of nutrition (in order to ensure their nutrition), they follow the common path of he nerves of these organs. For this purpose they extend from the chain to the mixed rachidian trunk, by following the communicating branch in the opposite direction to that of the fibres coming from the spinal cord, and, having arrived at this trunk, they follow it towards the periphery to finally reach the contractile or secretory elements for which they are intended. A nerve like the radial, the sciatic, or the trigeminal, is thus mixed, not only because it contains sensory and motor elements of the conscious or voluntary order, but also because it contains others belonging to this unconscious or sub-conscious system which the great sympathetic helps to characterize.

Its sensory elements.—In the preceding description we have endeavoured to trace an involuntary motor fibre from the cord to its termination, in the direction of its conduction. The great sympathetic contains, together with these motor fibres, sensory elements which duplicate them and whose conductivity is naturally opposed; but having made this reservation, their arrangement should be the same. As a matter of fact, the constitution of the great sympathetic has been ascertained by experiments made on its motor portion; the sensibility of the organs of nutrition is too obtuse to be appealed to as a witness as experimental evidence; the sensibility known as reflex might serve for such a research which is still very little advanced.

Metameric arrangements: Ganglia.—The chain of the great sympathetic forms its axis or chief part. Its resemblance to the spinal cord is striking: as a rule there are on each side as many ganglia as vertebræ, as many communicating branches as nerve pairs. Yet, in the cervical region several of these ganglia coalesce, the number being reduced to three for seven vertebræ. Of these three ganglia there is one (the first thoracic, still known as the stellate ganglion) which represents a fusion of ganglia, some of which belong to the inferior portion of the cervical region, others to the superior portion of the thoracic region. Above the superior cervical ganglion, the great sympathetic chain seems to disappear and to be entirely absent in the prolongation of the spinal cord known as the bulb or the medulla oblongata. In reality a trace of it has been recognized in the anastomosis which proceeds from the superior cervical ganglion to the Gasserien ganglion: this is at least the conclusion at which I have arrived as the result of my dissections and my experiments on animals, in which this anastomosis has more importance on account of the predominance of the face over the brain. From the Gasserien ganglion, the fibres of this anastomotic branch follow the branches of the trigeminal, which they once more leave in order to reach the ganglia annexed to these branches (ophthalmic, spheno-palatine and otic ganglia).

Cranial Sympathetic.—In this region the sympathetic chain has the same relationships with the medulla oblongata as lower down with the vertebral spinal cord. By the roots of the trigeminal it receives new origins from the bulb, while it supplies branches of distribution to the branches of the trigeminal,

coming from below (from the spinal cord), and which proceed together to the organs placed in the field supplied by this nerve. Above this point, still other nerves, the motor nerves of the eye, supply to it small branches of similar origin, such as the large and short branch of the oculo-motor nerve. Below, that is to say, between the trigeminal and the first cervical pair, the connexions of the chain with the bulbar nerves, such as the facial, the glosso-pharyngeal, the pneumogastric and spinal accessory, are but little obvious, or are reduced to insignificance. This is not the same thing as to say that these nerves are not related to the great sympathetic; only these relations are effected in a less simple manner, less systematically than with the trigeminal, in which the aspect of a spinal pair is still recognizable, and especially as regards the spinal roots.

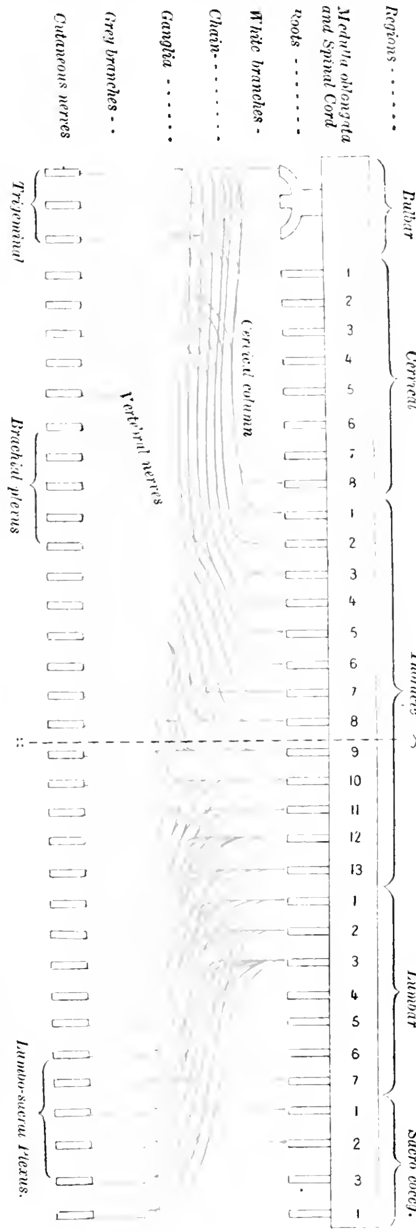


FIG. 122.—Diagram of the great sympathetic representing its cutaneous distribution and its two orders of fibres projection.

On the right of the diagram the medulla oblongata, the spinal cord and their roots. On the left, the cutaneous nerves containing these roots (chosen on account of their more regularly metameric distribution). In the middle, the ganglia of the sympathetic chain. These ganglia give off branches of distribution (in blue) which join the cutaneous nerve belonging to the same metamere as the branch itself and the ganglion which has given it off. On the other hand, these ganglia receive branches of medullary origin (in red) which arise from segments of the spinal cord situated either higher or lower than the corresponding metamere.

Spinal origins condensed in the thoracic region; supplementary origins in the medulla oblongata and the sacral spinal cord.

Symmetrical arrangement with regard to a plane *xy* cutting across the middle of the thoracic region.

The facial, by its small root (nerve of Wrisberg), supplies fibres which, like the two petrosal and the chorda tympani branches, proceed to the spheno-palatine, otic and sub-maxillary ganglia and manifestly come from the origins of the great sympathetic. The glossopharyngeal, by its branch of Jacobson, gives off similar filaments. As to the pneumogastric and spinal accessory, these large nerves

form only moderately fine anastomoses with the chain at the superior cervical ganglion, but, further on, a large portion of their fibres pass into the pharyngeal, œsophageal, gastric, pulmonary cardiac plexuses, while their terminations form, in the abdomen, one of the most important origins of the solar plexus. The hypoglossal much resembles in its constitution the arrangement of a spinal pair as regards its connexions with the great sympathetic.

Its bulbar origins.—In these bulbar nerves, which seem to elude the typical arrangement of the spinal roots, and to which for this reason special names have been given, instead of simple numerals, this arrangement when sought for is practically found to be present; it is obvious, whether it is a question of the relationships, of sensation to movement, or whether of those which connect the voluntary to the involuntary nerves for the performance of functions as a whole. The difference lies especially in the fact that, in the regions of the organism (thorax, abdomen) in which the metameric division of the vertebræ is recognizable at first glance, similitude of form justifies the inference of similitude of function directly experiment has determined this as concerns any one of these metameric groups. In localities where this arrangement has been upset by new superadded formations (skull), such an inference is impossible, and as regards each nerve, each nerve branch, this function must be determined by experiment. It is for this reason that there is a series of nerves called *cranial*, which are not included in the general formulæ comprising the grouping of nerves of different functions, formulæ based on experiments carried out on the spinal nerves. The nature of this grouping is in no sense absolute; the separation into metameres does not express an absolute physiological necessity, but a fact of development, of evolution, the reason of which lies in the past. Whether these conducting fibres are gathered together into bundles more or less numerous, more or less voluminous, or more or less resembling one another, is of little importance as concerns the function; the essential point is that they have, individually, relationships which are appropriate to their origin and to their termination; the rest is contingent.

Myelinated and non-myelinated fibres.—The fibres of the great sympathetic are *myelinated* fibres, usually *of small diameter.* Near to their cell of origin and near to their termination they lose their myelin sheath, which has led to the formation of a category of fibres known as *those of Remak* or *non-myelinated* fibres, which were formerly considered as being special to the great sympathetic; they are but prolongations of the first. This arrangement is not, as has been thought, peculiar to the great sympathetic, but is merely much exaggerated in it. When these non-myelinated fibres predominate over the others (as in the neighbourhood of the ganglia), the nerves assume a greyish colour which encroaches on the ordinary whitish colour of nerves.

White and grey branches.—Onodi and Gaskell have noticed that the communicating branches which unite the mixed spinal trunk to the sympathetic chain, are, some of them, whitish and others grey. The first would especially contain the fibres of origin, the second those of distribution. The communicating branches of the thoracic region are white; they represent especially *fibres of origin* which effect a connexion between the cord and the chain; those of other localities, in proportion as we get farther away from the thorax, are *grey*: they especially represent *fibres of distribution* proceeding from the chain to the organs. These facts are in accord with the remark which I have previously made, based upon experimental data, that *the origins of the great sympathetic are especially condensed in the thoracic region of the spinal cord.*

Ganglia; grey matter.—The ganglia of the great sympathetic, studied by the new methods, present the general structure and character of grey matter. It has long been known that they contain *nerve cells* (the body of the cells of

the neurons). It has since been ascertained that they also contain ramified prolongations which radiate around these cells and cause them to resemble those of the cord and of the brain. It is also admitted that these prolongations have *free terminations*, which come in contact with the axis-cylinder ramifications of the neurons which carry the impulse to them.

These are all characters which draw together the ganglia of those nervous organs which are known as centres, and they are in unison on the other hand with the data concerning them furnished by experiment.

In a sense, they are localities in which nerve conductors are interrupted or, which amounts to the same thing, sites of association for neurons which enter into the constitution of this system in view of its special functions. It is this which essentially characterizes the grey matter of the ganglia; the ganglia of the great sympathetic are nothing more than one of the special areas of this substance, attached to its other areas by links such as those which, in the so-called cerebro-spinal mass, unite the grey axis of the cord to the cerebral cortex. It would be of the highest importance to be acquainted with the laws, whether general or special to each group, according to which this association is effected. There is still very little known about it: nevertheless, experiment has furnished some facts which are of an interesting nature.

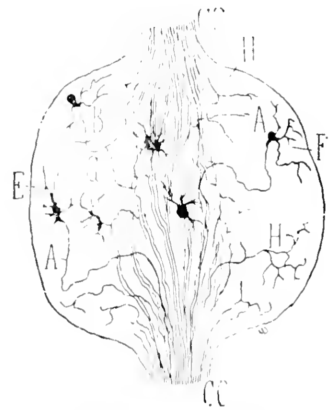


Fig. 123.—Thoracic ganglion of the embryo of a fowl (after Cajal).

A, B, cells whose axis cylinders sink in the chain CC: E, F, protoplasmic prolongations; G, collaterals; H, terminal ramifications of the axis cylinders.

Isolation and Dependence.—Observing the ganglionic chain of the great sympathetic, with its typical and regular form, its situation outside the vertebral column and its prolongations to the visceral organs, one is tempted, by exaggerating somewhat the conception of Bichat, to regard it as an independent system, that is to say, one whose function is independent of that of the rest of the nervous system. Experiment has refuted in different ways this absolute conception. The influence of the spinal cord, and even of the brain, is transmitted to the viscera through the great sympathetic, which is a proof of a somewhat close bond of union between these different assemblages. An opposite opinion, also obviously exaggerated in the sense of simplicity, would regard the great sympathetic as an ordinary conductor without special influence on the impulses which pass through it. The truth is *that the great sympathetic represents systematized groups, connected with other analogous groups, with which they are neither constantly fused, nor from which constantly isolated, but from which it is possible* to isolate them; the bond of union being either made or broken according to functional necessities. Experiment shows that they are capable of isolation, by manifesting in them complex nerve acts, such as the reflex or inhibitory actions. In the normal exercise of functions, this isolation has also, at certain instants, its *raison d'être*. In an aggregate so essentially mobile as the living being, dependence or independence is not fixed and invariable, but is, on the contrary, mobile, contingent and graduated.

Study by degeneration.—The method of Wallerien degeneration (degeneration after section of the segment separated from the nerve cell of origin) has been made use of, concurrently with the ordinary methods of experimental physiology, in order to study the connexions of the sympathetic ganglia, either with other

centres, or between themselves. Schiff, having destroyed in birds the roots of the spinal nerves, found degenerated fibres in the great sympathetic; he naturally concluded that this latter has its origin in the spinal cord, in opposition to the views of those who located it in the ganglia.

Once again, it must be pointed out that these two opinions are not exclusive the one of the other. *The great sympathetic has cells of origin in the spinal cord and also in the ganglia. These cells are the place of origin of two orders of neurons, the one superposed on the other, which transmit the impulse to the ganglia where their junction is effected.* To make use of a comparison which renders this arrangement clear, there are motor nerves of the great sympathetic as there are those of the life of relation; the origins of these latter are not situated totally and exclusively in the brain or in the spinal cord; they are in the cerebral cortex, whence arise the fibres descending to the grey axis of the cord, and they are in this grey axis itself, whence the impulse returns to proceed to the muscles.

In the one as in the other case, there is a *superior* and *inferior* neuron. In that which is known as the great sympathetic, the superior neuron commences in a cell of the grey medullary matter. According to Pierret, this origin should be found in the *tractus intermedio-lateralis* (middle horn), a species of third horn interposed between the two others. This neuron follows the communicating branches and terminates in some ganglion. The inferior neuron commences in a cell of a ganglion and proceeds to the motor or secretory element for which it is destined.

The great sympathetic contains, in addition to the ganglia of the chain, *terminal plexuses of ganglionic nature* (for example: plexus of Auerbach and of Meissner in the intestine, the œsophageal, pharyngeal, cardiac, pulmonary plexus, etc., etc.), and it presents as well, in the course of its chief branches of distribution, more or less plexiform ganglia (for example, semi-lunar ganglion and solar plexus).

Between these ganglionic masses thus scattered from the vertebral column to the viscera, no other difference so far has been noticed than that affecting their situation; their structure and function are the same, so far as is known.

Terminal fibres and fibres of passage.—Are all these ganglia places of junction between successive neurons? Yes, in the sense that all contain cells of origin for a certain number of neurons. But no, in the sense which is sometimes implied, that all the fibres are interrupted in all the ganglia, and that there would be as many points of severance as of ganglia on the course of each conductor. Histology teaches us that in each ganglion there are, alongside the *terminal* fibres, *transitory* fibres, that is to say, those which pass on without stopping in the ganglion. In short, for a given fibre, the number of ganglia placed on its course does not imply the number of points of severance or of relays which interrupt it, these relays being effected in one or other of the three orders of ganglia indicated above (ganglia of the sympathetic chain, terminal ganglia, intermediate ganglia). This point cannot be determined precisely, all that can be said is that, *from the cord to the viscera there is at least one interruption, therefore at least two neurons which are successive or superposed.* However, *the transitory fibres, which pass through the ganglia* without exhausting their terminal arborization in them, *usually yield up to them some collateral branches,* which still further complicates this structure, but which helps us a little in determining its significance.

By this means a given fibre (a neuron issuing from the cord) distributes the

impulse to several terminal fibres (neurons arising from different ganglia). The law according to which this distribution is effected is unknown, both as regards the great sympathetic and the cord; it cannot be simple inasmuch as it represents functions necessarily complex. The associations which are effected in the grey matter, both ganglionic and spinal, are intended for the establishment of different and multiplied connexions, a sort of conflict between the neurons which end in this grey matter and start again from it, whence results a transformation of the impulse which is appropriate to the functions to be fulfilled. Very far from the impulse passing simply from one fibre to the following one, the field of distribution of every neuron, from its origin to its termination, must assuredly be very complicated as regards its relations with preceding or successive neurons, or even with collaterals.

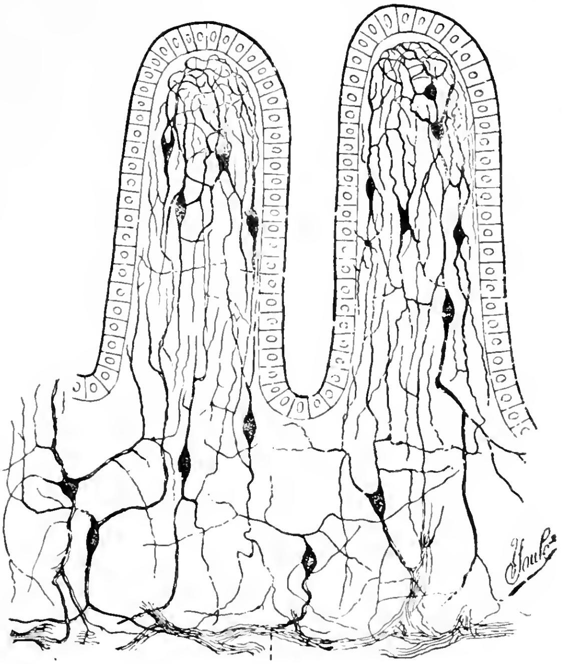


FIG. 124.—The interstitial sympathetic of the intestine (after Ramon y Cajal).

Section of two villi containing nerve cells of the great sympathetic.

2. The grey matter of the ganglia: its functions

The key to the systematization of the great sympathetic is to be found in the constitution of its ganglia.

Ganglia: motor nuclei.—These ganglia are *motor nuclei*, or, better, *sensori-motor*. Anatomically the origin of nerves having all the characters of motor nerves is found in them, in the sense that the neurons which form them have their cells ramified in these ganglia and their axons turned towards the periphery. The terminations of axons which come from above, and especially from the spinal cord, are also to be seen in them. Physiologically it is demonstrated that they are the localities in which the impulse is transformed. They may stop it, preserve it, redistribute it in a sort of way to organs situated in their field of innervation; each of them resembles a segment of the spinal cord. These essential points are acquired in a general manner; much

remains to be done as regards the study of the detail of these functions and the localized investigation of each separate ganglion.

Their experimental isolation from the Nervous System.—As regards many of the great sympathetic ganglia, their motor function may be demonstrated, but in no case more clearly and simply than in those of the heart. In this case a crucial experiment can be performed. The heart of a cold-blooded animal is separated by cutting the vessels which keep it in place (the vena cava and the aortæ); it is seen to beat with regularity for a considerable time; the lower two-thirds of the ventricle are separated with the scissors (the portion known as the apex); the ventricular portion thus detached immediately ceases to beat, while the pulsations of the superior portion (the auricles) continue.

Artificial circulation.—If it is desired to render the experiment still more striking, the gaping orifices of the cut vessels are supplied with glass cannulas; these are prolonged by indiarubber tubes full of blood, in such a way as to maintain an artificial circulation in the heart. The latter will drive the blood into a reservoir, whence it redescends into its cavities, and this circulation may continue for days; but if the physiological continuity of its nervous network be destroyed by a ligature applied a little below the base of the ventricle, the heart stops beating. In any case, the conditions which maintain this movement, comparable to that of the normal circulation, have disappeared; irregular and intermittent movements alone remain.

The heart deprived of its ganglia is thus, at the first glance, reduced to the condition of an ordinary muscle. It contracts if it is stimulated, but only when it is stimulated; except at the moment in which it receives the stimulation, it is inert. *When supplied with its ganglia, the motor organ receives stimuli without our supplying any to it: deprived of its ganglia, it ceases to receive stimuli unless we ourselves furnish them.* How can these ganglia contain a provision so inexhaustible that it can last for fifteen days, as has been observed? That these ganglia have preserved a portion of those impulses which have come from the cord by the cardiac nerves cannot be doubted; but that they have been reduced to this provision made in advance, seems difficult to maintain. Between these ganglia and the heart muscles, a reflex cycle is probably established whose centripetal paths (from the muscle to the ganglion) are unknown to us, as they have remained indistinguishable up to the present time amidst the other nerves; but it appears probable that they exist and that the beating of the heart maintains the stimulation of its motor nuclei by this mechanism at once reflex and automatic.

Engelmann and Fano incline, it is true, to attribute to the cardiac muscle, to the exclusion of its nervous system, the automatism of these cardiac movements. It must be admitted with them that the question is still enshrouded in obscurity, but it cannot be allowed that they have demonstrated that this automatism is purely muscular in the adult animal.

In the isolated stomach of the frog filled with a liquid alimentary material, such as milk, an experiment of the same nature can be carried out. A series of periodical contractions act on the liquid, and may be graphically recorded. The gall bladder acts in the same way, as Doyon has observed, as do all the hollow muscles furnished with ganglia.

The apex of the heart.—The apical portion of the heart, that which, after its separation from the ganglia, becomes immobile, has been, as we have said, compared to an ordinary muscle supplied with nerve endings, and which henceforth only contracts when it is artificially stimulated. To what extent is this comparison exact? It is precisely here that new researches have been undertaken,

and also at the same time a new and unexpected direction given to the question of the motor mechanism of the heart.

Its manner of reacting to stimuli.—In reality, viewed from certain aspects which it remains to examine, there is a great difference between the reaction of an ordinary muscle to a varied series of stimuli and that of this muscular segment, which is currently known as the apex of the heart. The ordinary muscle follows tolerably faithfully by its contractions the rhythm of the stimuli which are supplied to it, except that when they become sufficiently approximated it unites them into a sustained effort, which immobilizes it in its contraction, which then becomes tetanic. The apex of the heart acts rather in the contrary manner; it is in vain that the rhythm of the discharges of the stimulating alternate current are precipitated upon it: it refuses to respond to these stimuli and, after having accelerated its action up to a certain limit (which varies according to the intensity of the current), it continues to respond by dissociated rhythmical contractions; it *resists tetanization* (Eckhard). From one point of view the two objects are comparable; from another they are not.

Myogenous and neurogenous doctrines.—The rhythm, the automatism of the beats of the heart which gives such a special physiognomy to its movements, would not then have its explanation in the special organization of its nervous system, whether intrinsic or extrinsic, but, on the contrary, in the properties of the muscular tissue itself. Hence arise two doctrines which are maintained by physiologists on this important point concerning the nervous and muscular function. The first, faithful to the ancient conception, are the *neurogenists*: the second, partisans of the new explanation, are the *myogenists*. Both oppose each other by facts whether ancient or modern; both, in order to support a definite doctrine, are drawn into propping it up with hypotheses of which the gratuitousness or the spuriousness alone up to the present time impress the partisans of the opposite camp: on the one side as on the other conviction is complete. We will describe these two doctrines as briefly as possible, but also impartially.

Undefined paths of the propagation of the Impulse.—After Fick, Engelmann has observed that if a ventricle be cut in a zigzag form, the impulse, compelled to follow the course of the incision, none the less passes from one extremity to the other by this tortuous route. The heart is composed of muscular monocellular cells, which are often branched and welded together by a cement (*trait scaliforme*) at their extremities: thus these cells transmit the impulse from one to the other. It was originally thought that this muscular network of welded cells contained no nerve fibre; and the myogenous theory found in this fact a conclusive proof of its accuracy. Ranvier was the first to ascertain the existence of a very fine network, lining the preceding, a network the existence of which is rendered very obvious by the employment of the chromate of silver method. Deprived of this argument, the myogenists have found another of the same order in the facts furnished by comparative anatomy and embryology.

Movements of the heart in the embryo.—Fano, Pattrizzi, and Pickering have observed that in the embryo of the fowl the heart commences to beat not only before any nervous, but even any distinct muscular element can be distinguished. This is certainly a fact of the highest importance as regards the origin of the rhythm and of the automatism of the heart, whatever may be the solution of the question under discussion, whether for, against, or apart from myogeny or neurogeny. It is true that this information does not solve the problem, but rather brings forward a new one, namely, in a mass of homogenous protoplasm, manifesting the simplest functions of the adult heart, what is it which represents the muscle and what the nerves? The myogenists maintain as obvious that the muscle alone is represented, and that nerves will appear later at a certain

period of development. The neurogenists ask if our present methods of histological technique allow of our grasping a commencing differentiation; and if, with the improvements which they will undergo in future, the negative information concerning the embryonic heart will not have the same fate as that which was at first accepted for the adult heart; till recently it was not possible to distinguish nerve elements which are now easily demonstrated.

Excitability and conductivity.—The contraction of the heart is at the same time rhythmical and peristaltic. It arises in one area, starting from which it is propagated to other areas, like a wave changing its place. How is the communication of the impulse effected in this succession of cells welded together by their extremities? The myogenists maintain that, through the connecting material of these weldings, the sarcoplasm (not the myoplasm) of the muscular cells is continuous from the one to the other. According to them, the conductivity and the excitability of the muscular tissue would be two distinct things, the first localized in the sarcoplasm (primitive or organotrophic protoplasm of the cell), and the second in the myoplasm (differentiated protoplasm). Thus would be explained, as regards the myogenists, how it is that the wave of contraction, arising in one point, is sometimes propagated to remote points without affecting the intermediate area which remains in repose. The neurogenists object that the fact of propagation of the impulse, without visible movement, belongs particularly to nerves, and that there is no need to reject this explanation when it is a question of an organ like the heart, which is abundantly provided with nerves. It may be remarked, on the other hand, that the partitions between successive cells appear to be very complete, since they hinder in the heart the so-called current of demarcation or alteration, which in other muscles arises on their cut surface and persists up to the entire destruction of the muscle, thanks to the non-discontinuity of the latter (muscle of the skeleton).

The neurogenists maintain that the muscular element of the heart is absolutely inexcitable in a direct manner, and that every stimulus is conveyed to it through the nerves. This may also seem to be an exaggerated statement when it is remembered that, wherever a division occurs between nervous and muscular tissues, the muscle shows an excitability peculiar to itself. In truth, no stimulation is so efficient for it as that which it receives from its nerve. In the case of the heart we have no means of dissociation, because its nerves are found to be refractory to the action of curare. In any case, curare does not paralyse the cardiac movements.

So far as regards the propagation of the impulse from one portion of the heart to another, facts are already in existence which show that the auricle sometimes possesses a rhythm independent of that of the ventricle (Chauveau). Further, this independence can be obtained by section of certain nerve filaments which are visible on the surface of the heart (Nadine, Lomakine).

Periodic inexcitability; Refractory phase; Compensatory repose.—Peristaltism is the propagation of the wave of contraction; rhythm is its periodical reproduction in the same place at each point of its course under consideration. This periodicity is, as it were, the result of the incapacity of the heart to fuse together its contractions, a consequence of that which we have called its resistance to tetanization. As Marey has observed, during the active phase (systolic period of its contraction) it is *refractory* to every new or supplementary stimulus; during the diastolic period (that is to say, the period of loss of contraction) and the pause which follows it, it again becomes capable of stimulation. If the stimulus occurs in this diastolic period or during the pause, it gives rise to systole out of turn (extra-systole). But if this unrhythmical systole somewhat deranges the order of the contractions it does not alter the number of them, because it is followed by a compensatory repose. The stimulus has only anticipated the

contraction which should follow. The work of the heart remains constant. The fact of periodical inexcitability of the systolic phase is very real and evident; how is it to be explained? And is it to be attributed to the muscle or the nerve? The response may be foreseen according to the general theory accepted. For the myogenists it belongs to the muscle, for the neurogenists the complexity of the conditions which take part in it seems a clear indication of its belonging to the nervous system.

Point of departure of the stimulus.—The point of departure of the systolic contraction is in the sinus venosus and the auricle, whence the movement passes on to the ventricle. From the auricle to the ventricle it has been long thought that the passage could only be effected by means of nerve elements which proceed from one to the other. His, junior, having found that between the two a small bridge of muscular substance exists, the myogenists interpreted this fact in favour of the possibility of a transmission effected only by the muscular substance.

But the heart is double, and if, in the inferior vertebrata, it only contains one ventricle, it possesses two auricles, in which terminate, in one the vena cava, in the other the pulmonary veins, which are distinctly separated vessels.

It is from these very distinct regions that a double wave of contraction arises, of which the two courses, at first independent, finally converge on it or the ventricles. How can it be maintained, object the neurògenists, that, without the intervention of the nervous system, the muscles, separated at this point, can act so unanimously at the point of departure of the systole itself? (Hering.)

First origin of the stimulus.—Thus, for the myogenists, the rhythm, the peristaltism, in a word, the particular form of the motor reaction of the heart, is a purely muscular phenomenon. But whence come the stimuli? This is a doubtful point for them: but, they say, with sufficient probability it may be allowed, "that the stimuli do not take their origin in the ganglionic nerve elements, but rather in muscular elements which are histologically but little differentiated, . . . they are very probably the expression of the automatic disintegration of the living substance of a more or less extensive group of muscular cells, situated at the venous extremity of the cardiac tube." This time, the nervous system is dispossessed of the most fundamental and most essential property of those which up to the present time have been recognized in it, that of being an organ of stimulation for the other tissues. The cardiac muscle would not therefore owe its stimulus either to the blood or to the nerves; it would supply it to itself; by its own contractions it would be stimulated. Contraction and stimulation would thus be mutually related the one to the other, being, as they would be, bound together in an intramuscular, intracellular cycle. Such an exclusive opinion as this is not, however, that of all the partisans of the myogenous theory.

It cannot be allowed that the cardiac muscle receives the stimulus otherwise than by its nervous system. When the ganglia are intact, it is they which supply the impulse; when they are removed and when the apex of the organ is electrically stimulated, it is its nerves rather than its muscles which receive this artificial stimulation, and this in the same manner as an ordinary muscle. But—and in this it differs from an ordinary muscle—the effect of the stimulation is invariably rhymthical, that is to say, interrupted by intervals of repose; and peristaltic, that is to say, slowly propagated. The *origin* of the impulse being undeniably in the nerves, is the *form* which it assumes and which it impresses on the movement due to the nerves or rather to the cardiac muscle? In order to form an opinion, it is necessary to re-examine the three phenomena which we have described as periodic inexcitability of the heart, the extra-systole and the compensatory repose, in condensing as much as possible the conditions of their production.

Mechanism of the periodic inexcitability.—During the systolic phase of its

contraction, the heart is inexcitable.[1] As this systolic phase recurs periodically this inexcitability would also occur periodically. If the separated apex of the heart be artificially stimulated by the aid of discharges possessing the normal rhythm of the heart, every superadded stimulation falling on the systolic phase will be without effect. But every stimulation falling apart from this phase might produce an extra-systole. The rhythmical discharges supplied to the apex of the heart here seem to replace, purely and simply, the stimuli supplied normally by the sinus venosus (ganglia); the intercalated stimulus so far as concerns them behaves in the same way as it does with regard to the normal stimuli starting from the sinus. If, instead of giving to the stimulating charges the normal rhythm of the heart, they are rendered more and more frequent, the apex of the heart will at first follow this new rhythm; but the systoles being more and more approximated, the phases of inexcitability will be the same. When they coincide, it will necessarily follow that the stimuli will be without result; only those will be efficacious which are not synchronous with the systolic phase of subsisting contractions. Thus is explained, by means of systolic inexcitability, the fact that the contraction of the heart is always rhythmical; or, as has already been said, that this organ resists tetanization.

There is, nevertheless, a condition which may in a certain degree counteract this inexcitability, this is the intensity given to the stimulus. It may shorten the phase of inexcitability; very strong intercalated stimulation may give origin to an extra-systole in case a more feeble one should not arrive. This is at least the opinion of Marey and of Dastre, contrary to that of Engelmann, who denies this influence of intensity.

We see clearly that the neuro-muscular organ refuses the stimulation at a certain moment which we are able to define (period of activity), and accepts it at certain others (period of repose); and this is the first datum from which we start in order to explain the greater number of the facts peculiar to the heart. Fundamentally, this result is inexplicable. We only endeavour to find out to what tissue it belongs. But nothing exactly indicates to us that this refusal as regards stimulation is peculiar to muscle or nerve. Thus the periodic excitability may appertain either to the first or to the second. It remains to inquire into the compensatory repose and the constancy of the work of the heart which appear to be the consequence of it.

Mechanism of compensatory repose.—Dastre was the first to ask the question whether this phenomenon will be observed by stimulating the apex of the ventricle, or whether it appertains only to the heart furnished with its ganglia, in which case it would obviously be of nervous origin. We have seen above in what it consists. The extra-systole which is produced by irritating the whole heart in the diastolic phase is not a supernumerary systole, it is only an anticipated systole; a compensatory repose replaces the following systole in its normal place and the work of the heart remains constant. On the other hand, the extra-systole which is provoked by stimulating the apex of the heart, when a stimulus is intercalated out of turn in the interval between the contractions, is not, according to Dastre, followed by a compensatory repose. This latter, therefore, would be of ganglionic origin. Gley has also determined the existence of this phenomenon in the heart of warm-blooded animals. Later, Kaiser has arrived at the same conclusion. On the other hand, Engelmann has endeavoured to diminish the value of these facts. According to him, the more or less prolonged repose

[1] More accurately, the inexcitability commences $0^{sec}\cdot 1$ before the commencement of the systole and finishes $0^{sec}\cdot 1$ before its end. This delay of $0^{sec}\cdot 1$ corresponds to a *latent period*. This is equivalent to saying that the mechanical phenomena of the contraction are retarded by $0^{sec}\cdot 1$ as regards the chemical phenomena which develop the energy necessary to its performance. The inexcitability exactly corresponds with the chemical phenomena of the systolic phase.

which (in the case of the entire heart) follows the extra-systole has not a really compensatory value, but is due only to the fact that the extra-systole is followed by a phase of inexcitability which annuls the effect of the impulse descending at this instant from the sinus and the auricles. If, says he, two extra-systoles are produced one after the other, the following systole will not be repulsed two degrees, but only one degree; whatever may be the number of extra-systoles, the consecutive repose remains the same.

The nervous Network of the apex of the heart.—If the nervous origin of cardiac excitation cannot be denied, it must be remembered that, so far as concerns the special rhythmical form of the contraction which follows, there may be hesitation as to whether it should be connected with the muscular or nervous tissue. Certain facts, however, seem rather to attribute it to this latter. The apex of the heart is not exactly comparable to an ordinary muscle supplied with its nerve terminations. The nervous network which anatomy reveals in it displays a complication which these latter certainly do not possess to the same degree. Separated from the ganglia, properly so called, to which appertains the co-ordinating function of the cardiac contraction, this network still manifests to a certain degree their functions and properties. Sometimes, indeed, it appears to completely supplement them; this occurs when the section separating the ventricle from the auricle is effected very high up, immediately below the lowest group of the ganglionic cells. It may then happen that the ventricle, placed in favourable conditions, may begin to beat spontaneously. The organization of the excitation, its regular maintenance, would then be less the result of the ganglionic cells themselves than of the associations which their prolongations effect. In brief, the properties attributed to the ganglia would be rather those of the network which takes origin in them (Morat).

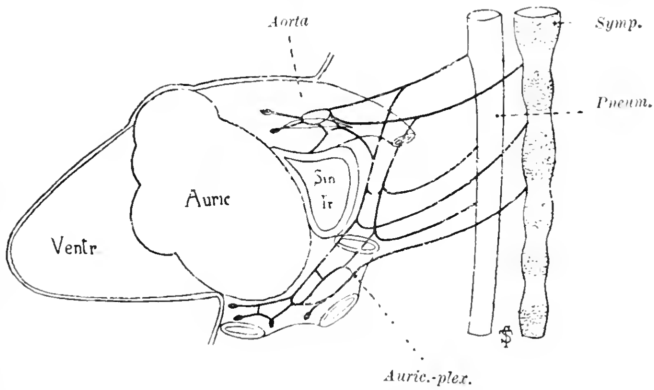


FIG. 125.—The cardiac plexuses in the human embryo (after W. His, junior).

Its complexity.—The difference between the apex of the heart and an ordinary muscle consists especially in this, that in the latter the nerve terminations are simple conductors deprived of any special arrangement by which they are united amongst themselves; while in the first, these terminations are systematized in such a way as to impress on the impulse numerous and very deep transformations. While in the case of a skeletal muscle the conflict of nervous actions of diverse sorts, which must determine the form of its movement, is carried on in the grey matter of the spinal cord, in the cardiac muscle this conflict between different nerve elements occurs in immediate contact with the muscular substance, and this is without doubt the reason why this special muscle seems to be so markedly different from all others.[1]

[1] The intestine and a number of organs of vegetative life in this respect much resemble the heart. The mesenteric plexus is in direct contact with the muscles of the intestine.

Its different origins.—The fibres which form the nervous network of the apex of the heart certainly arise in large proportion from the ganglionic cells situated at the base of the organ. They are the axons of these ganglionic cells, a species of very short peripheral neurons, which are, as has just been said, co-ordinated into a small system which is capable of automatic autonomous functional activity. In these ganglionic cells the terminations of the fibres of the great sympathetic and of the branches of the vagus destined for the heart come to an end, forming as they do, above the first, an exciting and regulating system of movement, a system of neurons of the second order. Some authors nevertheless maintain that the network of the apex of the heart may contain fibres arising either from the vagus or from the great sympathetic, and it may be allowed that this is so without any infringement of the general law which expresses the relationship of the deep and peripheral neurons.

It is known, indeed, that the plane of separation between the first and the second does not reside usually in a single mass or in a single ganglionic group, but exists at the same time in the majority of the ganglions arranged in graduated series in the course of the nerves proceeding from the cord and from the bulb, in such a way that, side by side, with short peripheral neurons (cells situated in the heart), there are long peripheral neurons (whose cells of origin are situated in the sympathetic chain or in the vagus). On the other hand, so far as specially concerns the cardiac ganglia, the surface of separation between the peripheral and deep neurons is not necessarily in the immediate neighbourhood of the ganglionic cells, but may be found represented in the nervous network which emanates from them very near the muscular element.

Anodic stimulation: its inhibitory effect.—In the manner in which it responds to stimuli, the heart also presents the following peculiarity noticed by Biedermann. Let a ventricle containing blood whose pressure upon its walls is moderate be taken.[1] The ventricle is stimulated by the unipolar method; that is to say, one of the poles of the circuit of the battery being placed on the body of the animal (frog, turtle), the other pole is placed in contact with the apex of the heart. The resulting effect is not only different, but is inverted, according to the nature of the pole which touches the ventricle. If this is the negative pole (cathode) the locally stimulated portion contracts according to the well-known law which has been established by the observations of Chauveau; if it is the positive pole (anode), the locally stimulated portion becomes distended by the pressure of the blood. It must be admitted that before any action of the stimulating current the ventricle was in a state of tonus: the action of the negative pole or cathodic stimulation has increased this tonus, the action of the positive pole or anodic action has diminished it.

Antitonic action of the vagus nerves.—The diminution of tonus which thus results from anodic excitation has been very naturally regarded as an inhibitory phenomenon, and this so much the more as the stimulation of the vagus may give rise to altogether analogous results, though generalized in the heart as a whole. If in the turtle one of the vagus nerves is stimulated in the neck, the intensity being just sufficient to produce arrest of the ventricular contraction, and if, during this arrest, the vagus of the other side be stimulated, the line of tracing on the right side will fall slightly below its primitive level and will thus

[1] Immobility of the apex of the heart is obtained by its *physiological separation* from the rest of the organ. It is not necessary that this separation be effected in the mechanical sense of the word. It can be obtained by placing a ligature tied round the upper part of the ventricle, in which a cannula has been placed and on which the constriction of the ligature acts. This cannula is in general communication with a tube filled with blood, or with serum playing the part of a manometer.

remain during this double stimulation. This is a device for rendering evident the *antitonic action* of the pneumogastric (Dastre and Morat).

The inhibitory action of anodic excitation applied directly to the ventricle is differently interpreted according to the views of the observer. For a thoroughgoing myogenist, the action is exerted on the muscle itself. For the neurogenists, it affects the nervous tissue; but it may be differently interpreted according to whether it is maintained that the fibres of the vagus have a direct inhibitory influence on the cardiac muscle, or whether these fibres are regarded as exercising their inhibitory action on the tonic stimulation distributed to the muscle by the intraventricular nervous network. This network is, indeed, complicated, and it is justifiable to conceive it as formed of elements acting the one on the other, or the one by the intermediation of the other.

Conclusion.—In brief, if certain facts of great importance are put on one side, such as the loss of motor spontaneity in the portions of the heart separated from the ganglionic apparatus, it is seen that, whatever interest attached to the numerous discoveries concerning details which have been made in seeking to investigate the mechanism of the cardiac motricity, none has a really decisive value as regards the solution of this problem. The functions of the muscle and of the nerves continue in some degree indissociable by our present means of analysis. Consequently the arguments drawn from analogy with other motor systems in which dissociation is possible and even easy, have a great influence. They manifestly plead in favour of an explanation which as a whole is practically neurogenistic.

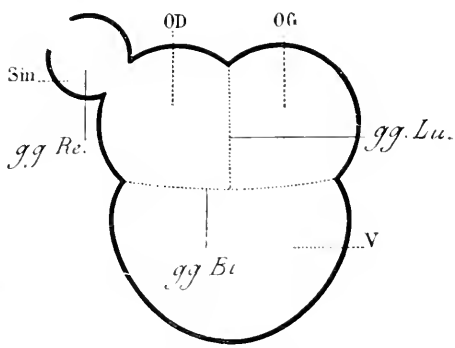


FIG. 126.—Ganglia of the heart in the frog.

OD, OG, right and left auricles; V, single ventricle; *Sin*, sinus venosus; *gg.Re*, ganglion of Remak; *gg.B*, ganglion of Bidder; *gg.Lu*, ganglion of Ludwig.

Functional rôle of the different ganglia of the heart.—In their totality, the cardiac ganglia have a motor action as regards the heart. Their isolated functions are not the same for all. Situated, the one in the sinus venosus (ganglion of Remak), the other in the interauricular partition (ganglion of Ludwig), the third in the auriculo-ventricular partition and the upper portion of the ventricle (ganglion of Bidder), they are adapted for experiment involving their separation or isolation. If a ligature be placed at the line of separation of the sinus venosus and the auricles, the heart immediately stops beating; this stoppage may last for a quarter of an hour or twenty minutes, then the beats recommence. This is the experiment known as that of Stannius. It is one of the most significant of the numerous ligature experiments which this observer has performed in this kind of research.

It has been disputed as to whether this ligature acts as a blocking effected in the intracardiac nervous system, or by stimulating certain portions of the latter. In other words, does it suppress excito-motor centres? Or does it stimulate moderating centres or nerves? The two opinions are not exclusive the one of the other. The ganglion of Remak is situated in the locality in which the wave of heart contraction arises. It is this ganglion doubtless which supplies the initial stimulation whence this contraction proceeds. If it be thrown out of action, the two other ganglia remain for a time insufficient to give rise to new

contractions. And this so much the more as the ganglia of Bidder and of Ludwig appear to have a reciprocally antagonistic influence; the first being regarded as especially excito-motor, the second as especially inhibitory.

If, while the heart has stopped beating through the application of the first ligature of Stannius, a second be applied at the boundary line between the auricle and the ventricle, the heart also is seen to respond. Is the recommencement of the beats due to the suppression of the inhibitory action of the first ligature; to the suppression of the inhibitory action of Ludwig's ganglion; to the direct stimulation of Bidder's ganglion?

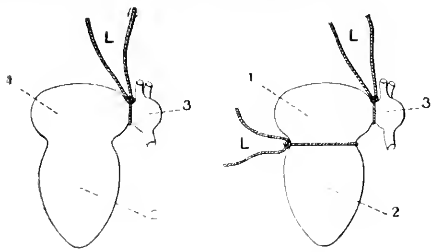


Fig. 127.—Ligatures of Stannius.

L, site of the ligature; 1, auricle; 2, ventricle; 3, sinus venosus.

Fig. on the left: ligature at the boundary of the sinus producing stoppage of the heart beats for some minutes.

Fig. on the right: second ligature applied after the first causing reappearance of the beats.

It is probable that all these influences act at the same time. There are different ways of proving that Bidder's ganglion is especially excito-motor; on the other hand, by directly stimulating Ludwig's ganglion through the thickness of the interauricular septum, stoppage of the heart results.

Reflex function.—It is invariably the case that, while the heart is stopped by the first ligature, if the ventricle be lightly touched, it is observed to contract. Bidder, who was the first to perform this experiment, regarded it as a movement of reflex nature whose centre of reflection would be situated in the still intact ganglia. On account of its special position in the depth of the muscular tissue, the intracardiac nervous system is little adapted for the demonstration of the reflex power of the ganglia; but there is no doubt that this power exists in it.

Division of attributes.—According to Cyon, the functions of the three principal ganglia are as follows: situated at the point of departure of the wave of cardiac contraction, the *ganglion of Remak* would control in the first place the *frequency* of the heart-beats; placed immediately above the ventricle and being prolonged into it by cells disseminated in its upper portion, the ganglion of Bidder would give rise above all to the *force* of the contraction; as to the totality of cells which in the interauricular wall forms what is known as the ganglion of Ludwig, it would possess a *regulative function both as regards the frequency and the strength* of the heart beats, and consequently would regulate the activity of the other heart ganglia.

Although these details, both anatomical and functional, have been more especially demonstrated in the heart of the frog, they are equally applicable to mammals, in which are found the more or less complicated equivalents of the preceding organs and of their special functions. Experiments analogous to all the preceding may be performed in them, on the condition that the properties of the tissues are maintained by artificial circulation; experiments, it is true, which are more difficult to carry out in the mammalian heart, on account of its interstitial circulation. Newell Martin and Langendorff have demonstrated circulations of this kind, confined to the heart itself, in the superior animals.

Action of oxygen on the movements of the heart.—If the movements of the heart depend on its ganglia, these latter in their turn depend on a number of conditions which influence their excitability. It is necessary to consider especially the gaseous condition of the blood and its temperature. These conditions

certainly act ont he muscle and on its nerves, but primarily and energetically on these latter.

The influence of oxygen on cardiac contractions is so obvious and necessary that this gas has been called the stimulant of the heart. It is perhaps more accurate to say that *it is indispensable for the maintenance of its excitability.* In warm-blooded animals it is the rapid exhaustion of oxygen which causes the heart, even when retaining its ganglia, to stop beating after a short interval when it is separated from the animal. In dogs submitted to a pressure of two atmospheres, and more in pure oxygen, the heart removed from the chest remains longer in a living condition (Cyon), doubtless because the provision of vital gas is greater in it. In cold-blooded animals, in which its consumption is less active, contact with the external air suffices to partially renew the provision of oxygen. A frog's heart, emptied of blood and placed in oil, quickly stops beating (Goltz). A frog's heart, in which an artificial circulation of serum is kept up, will stop beating when the quantity of oxygen contained in the serum is exhausted; it will recommence beating if the serum be changed; if the serum is coloured with a little hæmoglobin which transports the oxygen, the heart-beats will continue persistently (Kronecker, Rossbach). When the oxygen commences to give out, the heart presents a special periodic rhythm, which has been studied by Luciani, a rhythm in the course of which groups of pulsations are separated by pauses.

Action on the cardiac ganglia.—Oxygen is necessary for all the tissues; its privation will cause muscular as also nervous paralysis. But when a heart is asphyxiated, it is its ganglia which first suffer from this privation. This will be obvious from the following experiment. If, instead of the entire heart, the apex of the organ be adapted to the cannula of an apparatus for keeping up artificial circulation, and if its movements be excited by electrical stimulation, the deprivation of oxygen will no longer be followed by the prompt and characteristic results which ensue when the heart is beating automatically through the action of its ganglia. It is possible, indeed, to cause blood charged with carbonic oxide to circulate in the ventricle, which is consequently deprived of oxygen, and nevertheless the strength of the beats will continue during a certain time, which is almost the same as before (Julia Divine).

The special mode of action of oxygen on the cardiac nerve tissue is not determined. Some suppose that its rôle is above all to cause the disappearance, by oxydizing them, of certain waste substances arising from cellular activity (Richet).

Oxygen, apart from the directly *energetic* action which was attributed to it in the first instance by the experiments of Lavoisier, thus possesses another indirectly energetic, which may be called an *exciting* action, or one modifying the excitability. In both cases it causes an expenditure of energy, but in a very different manner. In the first, it follows a cycle of the simplest order (cycle of chemical reactions which give off heat and energy); in the second, it takes part in a cycle of the most complicated order (the cycle of nervous excitation) which, superadded to the preceding, plays in it the part of a power of disengagement capable of attracting the reactions which themselves make use of the greater part of the oxygen. This current through the organism of matter and of energy, following paths some direct, others more and more roundabout, is characteristic of the living organization and of its elaboration

The action of oxygen on the nerve centres is not, doubtless, fundamentally different from that which it exerts on the other tissues (the muscular for example). But, as the nervous tissue has in the animal organism a special situation which confers on it the government of the other tissues, it is obvious that this action is both more rapid and more evident.

Action on other centres.—Far indeed from being special to the ganglia of the heart, the action of oxygen is exerted on the whole of the nervous system, and especially on the grey matter. According to the organization of the latter, this action will have very different, sometimes even opposite effects. The oxygen which excites the movements of the heart, by the action which it exerts on its ganglia, causes the cessation or slowing of those of respiration by the opposite influence which it possesses on the bulbar centres of the respiratory function.

Thanks to the oxygen (to the gases of the blood), the respiratory activity and bulbar excitability are so related that one diminishes the other, and reciprocally. It is partly owing to this compensatory mechanism that the regulation of the respiratory movements is effected.

Action of carbonic acid.—Carbonic acid has an action on the respiratory movements opposed to that of oxygen, in the sense that while oxygen provokes these movements through its deficiency, carbonic acid restores them by its presence. On the other hand, while a want of oxygen in the blood favours inspiration, the presence of carbonic acid in the same fluid favours expiration. A similar inversion of effect is met with in the cardiac ganglionic system ; it is only necessary to remember that the effects of the two gases, from the fact that they are respectively converse, are opposite in the heart to what they are in respiration. It has been seen that the presence of oxygen is favourable to the movements of the heart. If this gas is wanting and the heart is plunged *intus et extra* into an atmosphere of carbonic acid, its movements become slower and rapidly stop. Is this paralysis or stimulation ? It is rather the latter. The heart, like the respiratory muscles, is submitted to two antagonistic nervous influences, the one excito-motor, the other moderator or inhibitory. These influences are represented in the cardiac ganglia, as they are higher up in the spinal cord and medulla oblongata, and make use of them, the first by the cardiac branches of the great sympathetic, the second by the cardiac branches of the pneumogastric, both having their terminations in the ganglia of the heart.

Medullo-ganglionic fibres of projection.—The motor ganglionic nuclei are united to the grey medullary axis by *centripetal* and *centrifugal* fibres which form, above the nervous system special to each organ, a second system called extrinsic with regard to this organ (although it would be rather intrinsic with regard to the nervous system itself). The analysis of a system of this kind has been specially made as concerns the heart. Its constitution is equally cyclic. There are found in it : (*a*) centripetal elements represented by an anatomically distinct nerve in certain animals, the *depressor* nerve, a kind of very prolonged anastomosis between the cervical cord of the sympathetic and the vagus (sensitive to the effects of the intra-cardiac blood pressure, this nerve conducts to the medulla oblongata the impulses which this centre reflects on the motor cardio-vascular forces, with the object of regulating this pressure) ; (*b*) centrifugal elements, which from the medulla oblongata and the spinal cord descend into the ganglia of the heart by the branches of the vagus and of the cervico-thoracic sympathetic. Of these centrifugal nerves the first are *moderator*, that is to say *inhibitory* as regards the cardiac movements ; the others are *accelerator*, otherwise *excito-motor* of these movements. Both differ profoundly from the nerves which terminate in the muscles, and which for this reason are called terminal nerves. It is obvious that they act on the intra-cardiac system, and by it only, on the muscles of the heart. It is by the intermediation of this system that the first moderate their action or arrest it, but only for a time, and that the second accelerate these muscles, but without ever producing tetanization. The accelerators increase the number but diminish the amplitude, the moderators diminish the number but increase the amplitude of the beats (Cyon). Whether the intra- or extra-cardiac system be investigated, a tendency to uniformity of the work

of the heart is observed, and this has been confirmed by all authorities (Marey, Dastre, Gley, Langendorff).

The two orders of fibres (excito-motor and those of arrest) present a sort of antagonism or mobile equilibrium between themselves, but the intimate mechanism by which this is effected is quite unknown.

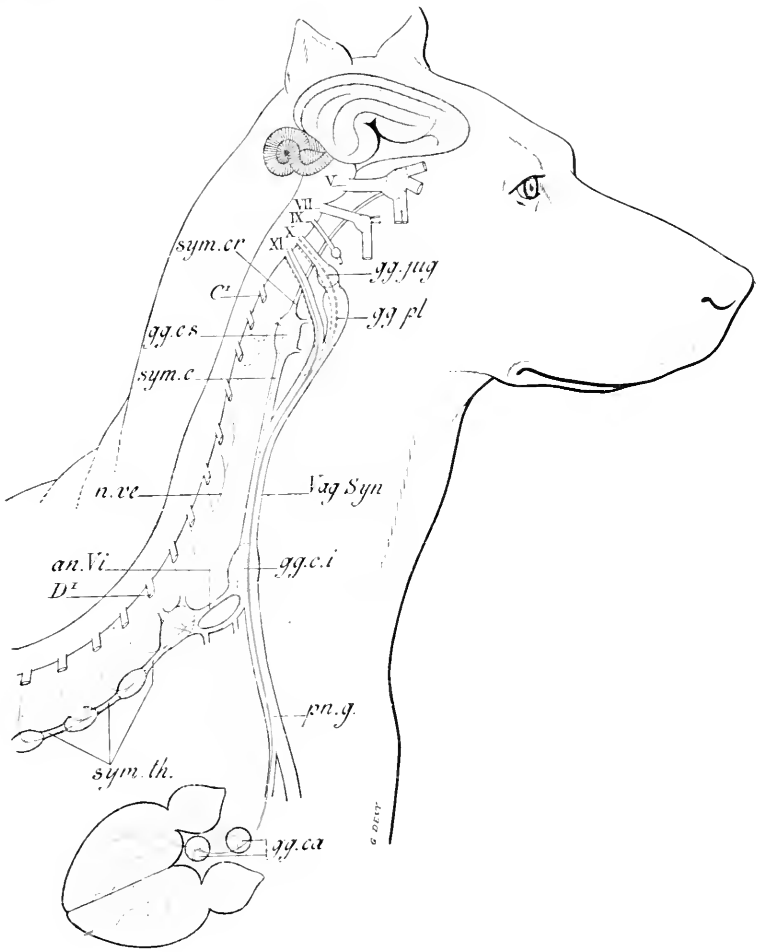


FIG. 128.—Diagram showing the innervation of the heart in the dog.

gg.ca, cardiac ganglia in which the cardiac nerves terminate; *gg.ci*, inferior cervical ganglion; *g.cs*, superior cervical ganglion; *gg.pl*, plexiform ganglion; *sym.th*, thoracic sympathetic; *an.Vi*, ansa Vieussenii; *pn.g*, pneumogastric; *n.ve*, vertebral nerve; *Vag.symp*, vago-sympathetic; *sym.c*, cervical sympathetic; *sym.cr*, prolongation of the sympathetic in the skull; C¹, first cervical pair; D¹, first dorsal pair; X, origin of the pneumogastric; XI, bulbar origin of the spinal accessory (the inhibitory nerves in red, the motor nerves in blue).

When the activity of the organ is no longer so regularly rhythmical the stimulus communicated to or maintained in it by its ganglia is called *tonic*, and examples of this form are numerous.

A. TONIC POWER.—It is well known what is meant by *tonus*, or the

light tension which is maintained in the muscles by a permanent current of weak excitation coming from the spinal cord so long as it remains in connexion with them, but which ceases when this current is interrupted by section of the conducting nerves. The same thing exists in the visceral muscles, in which the tonus is maintained as much by the spinal cord as by the ganglia. In order to estimate the share taken by these latter, all communication is at first suppressed between them and the spinal cord; the intensity of the motor phenomena is estimated. The ganglion itself is removed; once again this intensity is estimated; the diminution it has undergone in each case is noted. A good method of estimating it is to compare two symmetrical regions, of which one has been completely deprived of its nerve supply, while the other has preserved its ganglionic apparatus.

As evidence of this tonic activity of the ganglia, all phenomena depending on the great sympathetic may be taken: calibre of the vessels, redness of the cutaneous or mucous surfaces, dilatation of the pupil, condition of the cutaneous pigmentation, etc. Vulpian, Legros, Fr. Franck, and we ourselves, have carried out experiments of this kind, usually on the ganglia of the cervical chain of the great sympathetic. The conclusion arrived at is unanimous: *the tonic power of certain ganglia is incontestable,* and by parity of reasoning it cannot be rejected in the case of all similar ganglionic masses.

The ganglion has thus the power of accumulating in itself, by holding them in reserve, a certain number of impulses which it has received from all the fibres which are functionally united to it, which impulses come to it either from the cord or from the periphery.

Whether it is a question of a sphincter like the iris, or of tubes like the vessels, or, further, of contractile cells like the chromatoblasts of the skin, the tonic influence of the ganglia cannot be doubted. In frogs, this tonic action is very evident. In mammals it is very real. It has been clearly observed in the *superior cervical ganglion, the first thoracic ganglion, and the ophthalmic ganglion* so far as concerns the iris (Liegeois, Vulpian, Tuwim, Fr. Franck). It has been demonstrated in these same ganglia (except the ophthalmic) so far as concerns the vessels of the tongue (Vulpian), in the superior cervical ganglion as regards the vessels of the ear (Morat). These examples sufficiently prove that this tonic action is general, and that this would be established if it were sought for in other motor nuclei of the great sympathetic and the equivalent nerves.

Concerning the origin and the point of departure of this stimulus here made manifest in a sustained manner, and for a longer or shorter period after the isolation of the ganglia from their medullary connexions,

the same remark applies that has been made above, this point of departure probably consisting partially in a reflex impulse transmitted by centripetal nerves which are as yet indistinct.

B. Reflex Power.—Cl. Bernard was the first to suspect and to demonstrate experimentally the possibility of the occurrence of ganglionic reflex actions. He operated on the sub-maxillary ganglion. He cut the lingual nerve above its sub-maxillary branch (which passes through the ganglion of the same name) in such a way as to completely separate the superior centres from the subjacent system. By stimulating (electrically, not by the use of sapid substances) the tip of the tongue, he observed saliva issuing from Warton's duct. A reflex circuit was thus established between the tip of the tongue and the gland by the intermediation of the ganglion.

Schiff has contested the accuracy of this experiment; but Wertheimer, who has repeated it, criticizes Schiff's objections and rejects them. Langley observes that the ganglion which, in the dog, is called sub-maxillary is in reality the ganglion of the sub-lingual; the real sub-maxillary ganglion is made up of a mass of cells situated in the hilum of the gland of the same name. This anatomical detail, although displacing the centre of reflexion from one ganglionic mass to another, in no degree invalidates the conclusion of Cl. Bernard.

This experiment has since been repeated by several observers and applied by them to other ganglia, either of the chain or of the branches of the sympathetic.

C. Inhibitory Power.—In the exact sense which we attribute to this word, inhibition is the arrest of the movement about to take place, an arrest caused by an activity conflicting with that which originates this movement. For the stimulus which is projected into a nerve to have an effect so diametrically opposed to that which is recognized in it as logical and natural, it is necessary that on some part of the course it follows it should undergo a transformation of a more or less radical kind, by which its effect is changed. The ganglia of the great sympathetic form a locality of this kind. This has been demonstrated by Dastre and myself, by a characteristic experiment performed on the dorsal-cervical sympathetic of the rabbit.

Demonstration.—The *stimulation* applied to the cervical chain *below* the ganglia of the base of the neck causes *contraction* to such an extent as to obliterate the vessels of the rabbit's ear (Cl. Bernard, Brown-Séquard). A *stimulus* applied *above* these ganglia, to the thoracic chain in its superior portion, causes an enormous *dilatation* of these same vessels, that is to say, *inhibits the vascular tonus* (Dastre and Morat). A similar, but less constant, effect is observed by stimulating com-

paratively the lumbar chain above and below its first ganglia. These are the earliest experiments by which the phenomena of inhibition have been accurately localized.

Inhibition in the Invertebrata.—In the cephalopoda Physalix has observed the following facts. The pigmentary spots, the chromatophores, by their enlargement or contraction change the colour of the animal. The enlargement produces darkening of the skin by the spreading out of the patches; it is caused by the radiating muscles arranged round the chromatophore. The contraction of the chromatophores produces pallor: it is due to an elastic power opposed to the preceding. Stimulation of the pallial nerve causes the chromatophores to dilate by contraction of the radiating muscles (the skin darkens in consequence). Its section produces the opposite effect. The pallial nerve arises in the sub-œsophageal ganglia, which are thus centres for the chromatophores. Above the latter are the cerebroid ganglia. But these latter ganglia may exercise an inhibitory suspensive action over the first of such a nature that a stimulus, starting from these ganglia (directly or reflexly), causes pallor of the skin (by a cessation or loss of contraction of the radiating muscles of the chromatophores). When the cerebroid ganglia are separated from the sub-œsophageal ganglia by a section, this inhibitory phenomenon becomes impossible; stimuli, whether direct or reflex, uniformly produce darkening of the skin. Here again inhibition presents itself as a conflict *or a transformation of the impulses effected in a ganglion*, and consequently in the interior of the nervous system.

Various forms and aspects of the transformation of the Impulse.—The reflex power, the tonic power and the inhibitory power of the ganglia of the great sympathetic are not in reality three distinct things, but three different aspects of the very general function of transformation of impulses which is delegated to them, and this function is an essential attribute of the grey nervous matter. The ganglia of the great sympathetic are neither more nor less than characteristic portions of this matter, disseminated through the organs instead of being condensed in a hollow region, but nevertheless connected with other divisions of this substance, as well as amongst themselves, by links analogous to the white tracts in the nervous centres.

1. System of the life of relation; System of the vegetative life: Resemblances and differences.—The two systems, the one known as the life of relation, the other as the vegetative life, in spite of their profound external difference, are constructed on the same fundamental type which, for the sake of clearness, it will be necessary once again to recapitulate. They are both composed of reflex arcs or superposed nervous circuits. These circuits differ as regards their situation and their relative importance, their connexion with unlike organs, and the very unequal development in them of psychical phenomena which are based on sensation.

The first has very elongated inferior arches, so long indeed that they enter by their apex into the cerebro-spinal cavity. On these inferior arches a highly developed and complicated superstructure is based, which expands itself in the upper part of this cavity. It is this which has caused the system to be known by the somewhat unsatisfactory

name of cerebro-spinal. The second has its much shorter inferior arches, all situated outside the vertebral canal and disseminated in the organism in more or less immediate contact with the apparatus which it encloses like a net: whence has arisen the notion of the older observers that it is the bond of union between their functional sympathies; this conception is not absolutely false, but it no more defines this system than the denomination of cerebro-spinal defines the preceding one. On these extra-rachidian arches a superstructure is also built up which is infinitely less developed and much less apparent than the preceding one, in which it proceeds to immerse itself in the region of the spinal cord, not without communicating with the brain, but without it being possible in this latter to make any categorical distinction between the one and the other system. Further, this distinction, which is so obvious in the peripheral regions, where the nerves come in contact with differentiated organs, must necessarily be less so in the deeper regions, where all the conducting paths converge in order to effect the unity of the living organism.

2. **Mechanical and chemical acts; Contraction, Secretion.**—The connexions of the great sympathetic with the component apparatus of the organism are numerous, varied and graduated, and new ones are daily being discovered. While, in fact, the relations *of the organism with the exterior* are effected by a single category of organs, the striated muscles, and by a single modality of movement, the contraction of these muscles, nutrition and the involuntary life of the organs which take part in it require a fairly large number of cellular acts differing greatly the one from the other as regards their intimate detail. Nevertheless, they may be reduced to two principal categories which are perceptible, some under a predominently *mechanical* aspect, which is essentially *muscular contraction;* others under an aspect which is rather *chemical*, and which brings about what we know as *glandular secretion*, or the elaboration of special products by mutual reaction of the component elements of the protoplasm.

Connexion of the two phenomena.—These acts are not as completely independent as might be imagined from these designations, because both the one and the other have for their first point of departure the molecular phenomena and the expenditure of energy excited by the nervous system in the protoplasm of the cells. Both manifest themselves finally by a displacement of substances, rendered visible by the flow of liquid which proceeds from certain glands, or, more obscurely, by the exchanges which every cell maintains with the blood.

Every organ indeed, if it be muscular, has an internal secretion, every gland produces a movement of liquid. Further, the glands

present a great variety of elements, comprising amongst them veritable muscular cells. And the contractile elements, also, which are under the control of the great sympathetic, present a variety and a graduation which are extremely marked, from the striated fibres of the heart muscle to the pigmentary cells, and even to the fixed cells of the connective tissue, which some observers suppose, and not without reason, to be influenced by the ganglionic nervous system. Between these extremes a transitional form is represented by the non-transversely-striated muscular element (fibre cells, smooth muscles), which is not special to organic life, since in many of the invertebrata these elements are the only ones which carry out the commands of the will.

3. **Specific stimulation of the sensory nerves of the deeply situated Organs.**—There is no doubt that the centripetal elements of the great sympathetic receive their excitation from special apparatus analogous to those of the superior senses and distributed either to the surfaces of the large cavities or in the depth of the organs. Up till the present time we are poor in anatomical data concerning this point.

Anatomical data.—Dogiel, who has made a very complete study of the elements of the great sympathetic, describes a variety of these elements whose very long dendrites proceed from the ganglion in which their cell is contained, become involved in a small nerve trunk and then place themselves in contact with the epithelial surface. These dendrites were at first regarded as axons; they are distinguished from the latter by their dichomotic division and by the absence of collaterals; they have some analogy with the cellulipetal prolongation of the sensory nerve of a spinal ganglion; in fact, at a certain distance from the cell these long dendritic prolongations are observed to be covered with myelin. Such elements have been met with in the heart, under the pericardial serous membrane; in the intestine, where their ramifications unite the mucous membrane with the plexiform ganglion of Auerbach.

4. **Experimental data.**—Popielski, Wertheimer and Lepage have performed experiments concerning the pancreatic secretion which demonstrate *ab origine ad terminum* a functional cycle of unconscious vegetative life, as also the more or less marked developments which this cycle may undergo in the interior of the nervous system. It starts in a specific stimulus and it terminates in a specific act, passing through nervous paths which experiment localizes at its will in systems whose dimensions and complexity differ.

Relation between the nature of the Stimulus and the work produced.—The injection of an acid solution (HCl. 5 per 100) into the duodenum excites the secretion of pancreatic juice, which may be observed appearing at the extremity of a cannula placed in the duct of the gland. In the normal condition it is the chyme impregnated with *the acid of the gastric juice* which provokes this phenomenon of secretion, and among

the properties of *the pancreatic juice its alkalinity* must be included, which neutralizes the acidity of the gastric secretion passing into the intestine. Other stimuli like ether (Cl. Bernard) or chloral (Wertheimer and Lepage) can provoke the reflex secretion, but in the way of general stimulation ; while the acid seems here to be a specific stimulus appropriate to the function (or to which the function is appropriated).

Not only in the duodenum, but also at a certain distance from the latter, in the superior third of the small intestine, the acid stimulation has the same effect. Below this point it is without action, either because the appropriate nerve terminations are wanting, or because the nervous paths of association are, from this point of view, lacking between the lower intestine and the pancreas.

Variable extension of the cycle.—It may be proved that the reflection occurs in a system which is sometimes purely local (limited to the intestinal organs), sometimes comprises the abdominal ganglia, and sometimes includes, further, the spinal cord and the nerve masses which overlie it.

(a) *Local Reflex.*—When the cœliac and mesenteric ganglia (even the spinal cord) have been removed, the acid stimulation of the duodenal mucous membrane provokes pancreatic secretion, evidently through a nervous path, *by a reflection of the stimulus on the special ganglia which anatomy proves to be present in the pancreas.*

This experiment is allied to that which is made on the ganglia of the isolated heart, but it is more convincing, in the sense that the operator is here master of the stimulus and that, instead of an automatic undecomposable phenomenon, an obvious reflex act is in question.

(b) *Ganglionic Reflex.*—When the cord is removed and the cœliac and mesenteric ganglia are preserved, the same reflex effect is possible ; but the participation of the ganglia referred to above can be demonstrated in it. If, indeed, the duodenum be separated from the small intestine by a strong ligature, stimulation of the small intestine (by injection of an acid solution) provokes the pancreatic secretion. The propagation of this excitation can no longer be local as in the preceding case, but requires the intervention of the abdominal ganglia (or even of the sympathetic chain) as the path of association of the two separated segments of the intestine and of the reflection of one on the other.

(c) *Spinal Reflex.*—When the cord is intact and its connexions with the intestine and the pancreas are maintained, there is no doubt that it may serve as the site of reflection for the impulses propagated from the one to the other. Not only the cord, but the bulb and the brain may take part in the regulation of acts of this order, although they are involuntary and unconscious.

5. **Mixture of stimulating and inhibitory influences.**—The system which reflects and co-ordinates these impulses is certainly complex, even when it is experimentally reduced to its smallest dimensions Like every other of the same class, it employs elements some of which *transmit* the impulse, while others *inhibit* it. It is remarkable that the force (and probably the number) of these latter progressively increases,

in proportion as the system becomes more complicated, in arriving at the abdominal ganglia and especially the spinal cord.

So-called paralytic secretion.—The most abundant secretion is not that which takes place with the concurrence of the cord, but is on the contrary that which the purely local cycle puts in action (Wertheimer and Lepage). The removal of the abdominal ganglia may suffice to cause a flow of pancreatic juice (Cl. Bernard) : this is known as *paralytic secretion*, it being regarded as a consequence of the dilatation of the vessels of the gland. It may with more plausibility be attributed to the suppression of controlling actions appertaining to the spinal cord.

The study of the functions of vegetative life demonstrates or leads to the suspicion that there are many examples of the same kind, in which it is necessary to allow that chemical or mechanical stimuli, through the intermediation of given nervous cycles, regulate nutrition or the movement of the parts. The larger number of the hollow muscles proportion their contractions to their state of repletion and, hence, of their tension or distension. The contractions of the heart are regulated by the condition of the blood pressure, with the aim in view of maintaining in a constant condition, by the intermediation of its sensory nerve, the *depressor* nerve. The composition of the blood is itself regulated by the stimulations arising from its aberrations by a mechanism of which the pancreatic secretion affords an example at the very entrance of the paths of absorption.

3. Special Functions of the Great Sympathetic

The great sympathetic can be resolved into a certain number of systems which are fairly exactly superposable (motor, secretory, each one subdivisible into different varieties : vaso-motor, sudoriparous, etc., etc.), in which the mixture of their fibres has often led to a confusion being made between them, but of which it is possible to demonstrate the independent reality. Physiology has different means not only of bringing them into action, but also of dissociating them, thanks to their elective affinities for certain poisons. Example : stimulation of the cutaneous nerves simultaneously modifies the circulation of the skin and the secretion of its glands. It may be asked if the secretion is not merely the consequence of the circulatory change (vaso-dilatation). But, if a weak dose of atropine (1 milligramme) be injected into the blood of an animal, stimulation of cutaneous nerves causes the same circulatory effects, but no longer excites secretion of the glands. Therefore the poison has paralysed the glandular nerves separately ; hence the latter exist independently of the vaso-motor nerves. These different functions have been successively discovered, and we cannot flatter ourselves that we know them all. It is probable that the great sympathetic presides over a large number of fixed

elements of the tissues, whose relations with the nervous system are not at the present time accurately known.

Historical.—It is in operating on the cervical portion of the great sympathetic, which is more accessible, that the principal discoveries concerning its functions have been made.

Initial fact ; Orientation of the conduction.—The earliest is that of Petit (of Namur) known as Pourfour Dupetit, who observed, as a consequence of section of the cervical sympathetic, those phenomena which are known as oculo-pupillary (sinking of the globe of the eye, contraction of the pupil) ; these phenomena are explicable, the first by the loss of tone of the inhibitory elements of the sphincter muscle of the iris, the second by the loss of tone of the muscular elements of the capsule of Tenon. This double mechanism was not only unknown, but was incomprehensible to the originator of this experiment, who observed the change in the aspect of the eye as a whole, but without inquiring into its mechanism. But by this observation he established a fact new and important for that epoch, namely that, *contrary to the other motor nerves which appear to descend from the brain, this latter ascends in starting from the spinal cord towards the head ;* this was to distinguish, by one of its most striking characters, the systematization of the great sympathetic as regards that of the other nerves.

Biffi in 1841 performed the counter experiment, consisting in stimulating the superior end of the cut nerve, which induces dilatation of the pupil and exophthalmos.

Vaso-motor function.—Cl. Bernard (1851) performed on this same nerve an experiment which is still regarded as classical. *Having cut the sympathetic in the neck of a rabbit, he observed that the temperature of the whole of the corresponding side of the head, especially of the ear, was remarkably raised.* On making the counter experiment by *stimulating the superior end, he observed that the temperature fell below the original temperature,* as Brown-Séquard had observed almost contemporaneously.

The announcement of this fact caused much astonishment. Of relationship between the temperature and nerve action, between a fact markedly physical on the one hand and a fact just as markedly vital on the other, none was clearly seen. Brown-Séquard and Waller called attention to the fact that this relationship was not direct. Section of the sympathetic paralyses the muscles of the vessels which are located in the field of distribution of the great sympathetic, and its stimulation causes them to contract. This nerve is not thermic in function, but *vaso-motor ;* it diverts the distribution of the blood from the deep structures to the periphery and thus transports the heat from

the warm regions to those which are cooler. Such is the real explanation of the experiment of Cl. Bernard.

It has an extreme importance, because it reveals both the unsus-

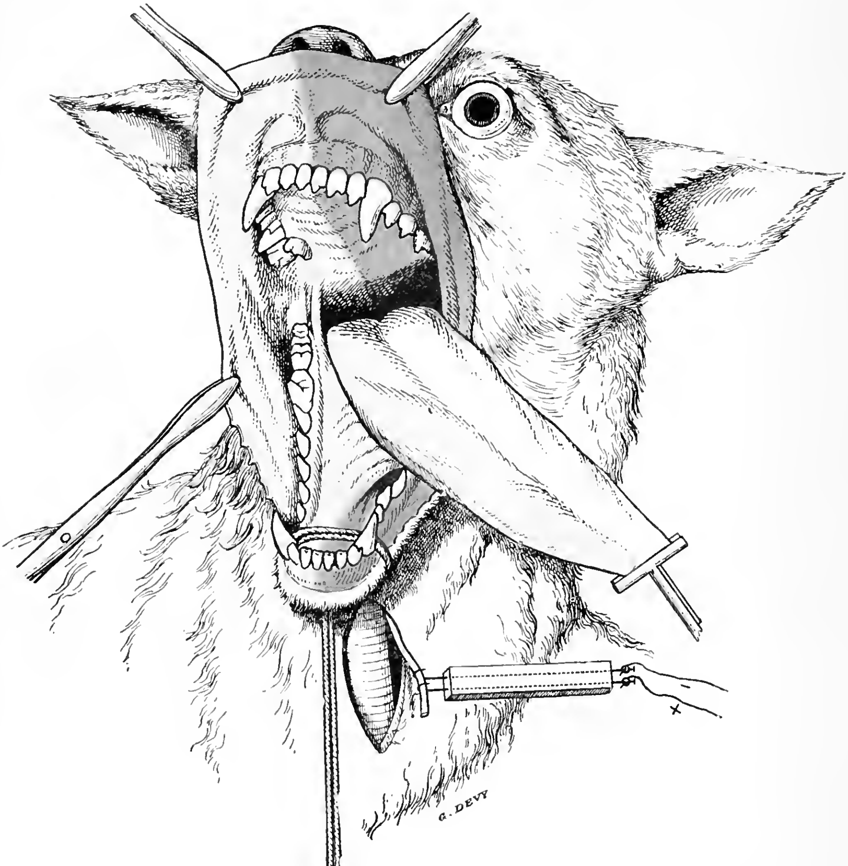


FIG. 129.—Effects of the stimulation of the cervical sympathetic in the dog.

The excitation is directed to the cephalic end of the common trunk of the vagus and of the sympathetic in the neck. The vagus has been previously cut at the base of the skull in order to eliminate the reflex effects to which it may give rise. Stimulation can also be brought to bear on the sympathetic at the point where it is separated from the vagus, either below the superior cervical ganglion, or at the level of the ansa Vieussenii.

Oculo-pupillary effects consisting in dilation of the pupil and projection of the eyeball.

Vaso-motor effects consisting in pallor of the tongue and ear on the side corresponding to the excitation (constrictive effect) and redness of the lips, the gums and the palatine arch on the same side (dilatory effect or one the result of inhibition of the vascular contraction). Jonesco and Floresco have confirmed this double vaso-motor effect in man.

pected, or very vaguely suspected, *existence* of vaso-motor nerves and also their *localization* in the great sympathetic.

Double Motor and Inhibitory Function.—Dastre and Morat in 1881 showed that stimulation of the great cervical sympathetic, in addition to the oculo-pupillary effects described above, and of the constriction

of the vessels of localities which are habitually obvious like the ear, *causes the dilatation of those of neighbouring regions, the upper and lower lip, the palatine arch*, and this very clearly in the dog. *Hence the sympathetic contains inhibitory vascular nerves.*

Cl. Bernard had previously shown (1858) by stimulation of the chorda tympani, the existence of nerves possessing the function of dilating the vessels. For this very reason the reality of the vaso-dilatory action of the great sympathetic was disputed, it being considered that the same nerve could not unite in itself two such opposite functions. But this functional antagonism between nerve elements belonging to the same group, is that which gives the chief interest to this experiment. On this account *the great sympathetic ceases to be a nerve like the others, and becomes in reality a systematized assemblage.*

Not merely, indeed, does it contain similar elements governing the circulation of neighbouring regions, but these elements are seen arising from different points of the spinal cord, converging the one towards the other, and in certain cases it is possible to point out the spot in which they influence one another.

Localization of inhibition in the ganglia.—We have called attention above to the manner in which the vascular results of stimulation change their character according as this stimulation is applied above or below certain ganglia of the chain (inferior cervical and first thoracic) situated on its course; how that which is made below has purely constrictive effects, while that made above is followed generally by those of dilatation, which in certain cases are intermingled with constrictive effects. By investigating separately some of the spinal origins of the cervical great sympathetic, others may be found of which some cause dilatation and others contraction of the vessels of the locality in question. From this it must be concluded that the motor nuclei of the vessels of the ear are situated in these ganglia, and that the branches which the latter receive from the thoracic spinal cord are fibres of projection, some excito-motor, others inhibitory. The stimulation passes from a superior to an inferior cycle, as when it is transmitted from the cerebral cortex to the spinal cord when the skeletal muscles are in question.

Secretory function.—In 1880 Luchsinger observed that stimulation of the cervical cord *causes an abundant secretion of the sudoriparous glands* in certain regions of the face (groin in the pig, muzzle in the ox), just as that of the dorso-lumbar sympathetic causes secretion of the glands of the hind-limb in the cat and dog. Czermak had already observed that stimulation of the cervical cord reacts on the *submaxillary* gland, causing a *very thick saliva* to flow from it; in both cases *the motor or secretory nerves of the glands* are put in action, this

being another species of nervous action which may be added to the preceding.

Cl. Bernard, in investigating the effects of the section of the cervical cord in the horse, had observed that the corresponding side of the face and neck was covered with sweat. But this phenomenon was then interpreted as being dependent on the vascular paralysis which follows this section. It is probable that it means something further, namely, the cessation of an inhibitory influence conveyed by the great sympathetic to the sweat glands.

Inhibito-secretory function.—Arloing (1890-1891), having cut this nerve in the neck in the ass, observed after some days that *the sebaceous glands of the external ear were crammed with their secretion*, and he regarded this result as being *one of the first observations concerning the inhibitory action of the sympathetic on the glands.* This author points out facts of the same nature relating to the *lachrymal gland* and to the *Meibomian glands.*

Function of accommodation for distant vision.—Morat and Doyon (1891) observed that stimulation of the same nerve produced not only dilatation of the pupil, *but a contemporaneous flattening of the crystalline lens*, which they recognized by the enlargement of the crystalline image (second image of Purkinje) at the instant of stimulation. From this they concluded that *the sympathetic governs accommodation for distant vision.*

Vaso-motor lymphatic function.—P. Bert and Laffont, by stimulating the mesenteric nerves, caused a contraction of the chyliferous vessels. Gley and Camus, operating on the thoracic sympathetic or splanchnic nerve, obtained variations of calibre of the thoracic duct and of the cistern of Pecquet (receptaculum chyli), generally, rather in the direction of inhibition, but also in that of constriction.

Pilo-motor function.—Stimulation of the sympathetic, especially in the trunk, causes *the hair to stand on end* in the corresponding cutaneous area. This effect, vaguely recognized by other experimenters, was observed for the first time in satisfactory conditions and described in detail by Langley, who has thus determined the pilo-motor function of the great sympathetic (1891).

Glyco-formative function.—By stimulating the great splanchnic nerve Morat and Dufourt caused an increased activity of sugar formation in the liver at the expense of the glycogen of this organ, and they observed that this effect is not directly subordinated to the hepatic circulation, which proves the existence of distinct nerves controlling the intra-cellular chemistry of the gland. This is an example of an internal secretion controlled by the nervous system.

Chromatic function.—P. Bert, experimenting on the chameleon, noticed the influence of the great sympathetic on the changes of colour of the skin, an influence which is equally observable in the frog after the removal of the ganglia of the great sympathetic (especially the superior cervical ganglion), as Vulpian has demonstrated.

Thus it is seen that the great sympathetic represents, as regards motricity, very different functions. While the voluntary nerves preside only over the striated muscles of the skeleton, the sympathetic has under its control a species of cells, varied and graduated both in form and function, which range from the muscular striated fibres of the heart to the glyco-formative cells of the liver, passing through the smooth muscles of the intestine and the vessels, and the contractile and secreting epithelia of the most diverse form and nature. While the voluntary system carries out these motor combinations (fundamentally also very numerous) by the aid of a single element, the muscular fibre, the involuntary system discharges its functions by the help of extremely differentiated elements. In the division which the two systems have effected of the component elements of the organism, the one has taken a portion of the muscular tissue, the other the remainder of the elements; whence the extreme importance of this latter in the primitive functions of the living being, and on this account indeed in the pathological study of these functions.

Methods of determination.—In order to distinguish these divers activities from each other and to discriminate at the same time between the nerve elements which correspond to them, recourse is had to methods which vary according to the circumstances. Examples: the contraction and dilatation of the pupil are directly observable, as also the erection of the hair; the contraction and dilatation of the vessels can equally be appreciated *de visu*, when an isolated artery is observed, such as the auricular artery of the rabbit. The condition of the capillary circulation in a superficial area (skin, mucous membrane) may be ascertained by the changes of *colour* of this locality, which becomes paler or redder according to the quantity of blood circulating in it (*colouriscopic method*). A less direct method, but one which is very accurate, consists in estimating and recording the *pressure* or the *rate* of the blood current in the arteries and the veins of the region whose vaso-motor nerves are stimulated or paralysed (*manometric* method). This method can be varied by measuring and registering the changes of volume of the region whose nerves are being studied (*plethysmographic method*). Both require that certain controlling facts be taken into account by which it is possible to distinguish a purely local from a general variation of the circulation. A method which has been highly prized for the study of the determination of vaso-motor phenomena consists in measuring the changes of local *temperature* corresponding to these actions on the nervous system (*thermometric method*); this method is very untrustworthy; the changes of temperature are very slow in their production and slow in dissipating, and they depend upon multiple and variable conditions, amongst which the changes which ensue in the local circulation are merely an isolated factor.

The contractions of the stomach and of the intestine can be appreciated and registered by the aid of various manometric or myographic apparatus. Slow movements appertaining to isolated cells, such as those of the chromatoblasts of the frog, can be recognized by examining under the microscope a transparent pigmented area, such as the interdigital membrane (*microscopic method*). The alteration of the general tint of the area can also be observed, and is included in the colouriscopic method.

The microscopic method, which has been long made use of in the study of the

circulation in transparent organs (especially in the frog), may be very advantageously employed for the special study of the vaso-motor nerves.

The *mechanical* phenomena of *secretion* may be recognized and estimated, like those of a circulation or of any flow of fluid, by the quantity of liquid produced, and its pressure in the conduits in a given time. *Chemical* phenomena require confirmation of another order, such as the dosage of the substances in the blood and the other humours, the test of the effect of ferments upon the substances which they transform, etc.

4. Systematization of the great sympathetic; its two orders of fibres of projection

The great sympathetic is formed of an intra-rachidian or spinal part and of an extra-rachidian or ganglionic portion, united the one to the

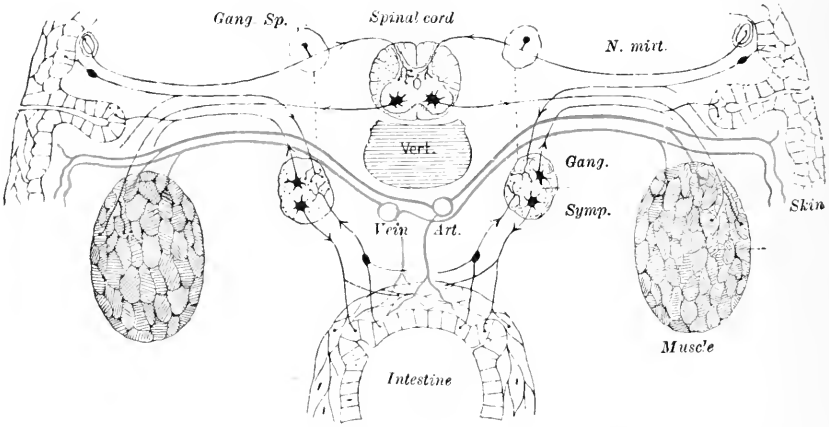


Fig. 130.—Diagram of a metamere, with its myelomere (completed by the spinal and sympathetic ganglia), its dermatomere, myomere and splanchnomere.

Penetration of the circulatory portion of the splanchnomere into the dermatomere and the myelomere. Circulatory parallel penetration of the elements of the great sympathetic. Mixture of these latter with the conscious voluntary nerves at the level of the mixed trunks.

other by its ganglia. These form two wholes comparable to those which, in the animal nervous system, connect, the one the brain to the cord, the other the cord to the periphery. Each of these wholes plays its part and has its special structure in both of these systems; but if in the two systems the arrangement of the deep nerves differs much, that of the peripheral nerves is very similar. Thus we once again encounter, in connexion with the great sympathetic and its ganglia the question, already considered, of metamerism, which arises once more.

Ganglionic Metamerism and Spinal Metamerism.—As regards the roots of the spinal nerves, we have drawn a marked line of distinction between the radicular metamerism and the spinal metamerism, the first being obvious and the other reduced to a mere trace. The inter-

vention of the great sympathetic tends still further to upset this latter in a new but quite as complete manner.

The ganglia of the sympathetic chain, with few exceptions, correspond, both as regards number and situation, to the mixed trunks of the nerve pairs with which they are united by so-called communicating branches. These ganglia, which have embryological and even functional connexions with the spinal ganglia, thus reproduce the primitive metamerism, the true metamerism; while the myelomeres have disappeared by fusion and reciprocal interpenetration, they have remained distinct. These ganglia of the chain give off by their communicating branches *fibres of distribution*, which follow the mixed trunks towards the periphery (these are the grey branches); on the other hand, they receive from the spinal cord *fibres of origin* by these same communicating branches (these are the white branches). But these fibres of spinal origin do not come from the pair of corresponding roots, they arise from roots situated either above or below the corresponding ganglion; and in order to do this they follow, in the chain itself, a more or less lengthy course, during which they usually pass over a certain number of ganglia.

If they are intended for the head or for the superior limb, they arise generally from the roots situated below those which are continuous with the nerve trunks of these regions; if, however, they are destined for the inferior limb, they take origin from roots situated above those of the nerves of this limb. This is the result of what has been said above with regard to the condensation of the origins of the great sympathetic in the thoracic region of the spinal cord, while those of the principal conscious voluntary nerves are found, on the contrary, in its cervical and lumbar enlargements.

However, besides these chief origins in the cord, the great sympathetic has others, which may partially coincide with those of the nerve trunks distributed to the region in question. For example: the sympathetic nerves of the face come to it from the five first dorsal roots, ascend by the cervical chain, reach the trigeminal, and, by its branches and ramifications are distributed to the apparatus and organs to which they belong; but, further, a portion of these nerves proceeds directly from the origins of the trigeminal themselves. The sympathetic nerves of the foot proceed to it from the three last dorsal and the two first lumbar nerves, and by the lumbar chain they rejoin the trunk of the sciatic nerve; but, further, a part of these nerves (by far the smaller) arises from the origins of the sciatic, that is to say, from the two last lumbar and sacral roots.

Between these two sites of origin, one principal and the other accessory, there is sometimes a very wide interval. As regards the sympa-

thetic nerves of the face, this interval extends to the whole length of the cervical spinal cord.

Parallel Systems for different functions.—The great sympathetic assumes or directs several functions: movement of the blood in the vessels, formation and expulsion of secretions, progression of the aliments in the digestive tube, etc. From this point of view, it may be resolved into as many parallel systems as there are distinct functions or species of cells for the performance of these functions. These systems, which we call *parallel*, are so in the strict sense of the word, in the sense, namely, that from their origin (spinal) to their termination, they are strictly superposable. Example: the ocular apparatus contains vessels, glands, and deep muscles regulating the access of light, which are all unconscious, involuntary organs. Their nerves, supplied by the great sympathetic, take their origin from the same regions of the spinal cord and bulb, whether they are vaso-motor, secretory, or dilator of the iris, etc. These origins, entirely superposable between sympathetic nerves whose functions differ, are, as is obvious, very distinct from those of the conscious voluntary nerves, which supply the ocular apparatus with sensation and movement.

Aberrant portions of the medullary segment.—In order to recognize spinal metamerism under its primitive form, it is necessary then, in an imaginary manner, to add to the spinal cord two formations situated outside the vertebral canal and which in fact appertain to it, namely, the spinal ganglia and the sympathetic ganglia. *Transverse superposed planes, which cut the spinal cord and the whole body, passing through the intervals between the nerve pairs, as also the communicating branches and the sympathetic ganglia, form the boundaries of a series of partial systems in which, nevertheless, all the essential functions of the nervous system are represented.* The spinal ganglia and the anterior cornua of the grey matter of the cord represent in them sensation and movement of animal life with the relations which they form together in the most simple reflex acts. The ganglia of the great sympathetic represent in them, by themselves alone, the sensation and movement of the vegetative life, with the relations which they effect in the ganglionic reflexes. These two associations are indeed slightly united between themselves (according to Dogiel), by the fibres of union which exist between the cells of the spinal ganglia and those of the ganglia of the great sympathetic.

Association of the Metameres by the tracts of the Spinal Cord and the connecting fibres of the Chain.—In brief, it is apart from the spinal cord properly so called, rather than in it, that we recognize primitive metamerism. The function of the cord is indeed the creation of associations of a new order very different

from those existing in the metameres. It associates mutually metameres of the life of relation and of them forms groups corresponding to definite functions. It is not under the necessity of associating the metameres (ganglia) of the vegetative life, because this association is effected apart from it, by the great sympathetic chain, which becomes by its connecting fibres the equivalent of the deep tracts, or those of association of the spinal cord. On the other hand, it associates amongst themselves, in their turn, the systems of animal organic life; the functions of the two orders being, as is well known, reciprocally dependent and compelled mutually to aid one another.

By examining matters from this point of view, we encounter under a new form the original difference of the two systems known as those of animal and vegetative life. In the segments of the juxta-ganglionic spinal cord defined above, we recognize once more, as regards the roots, the medullary origins of the nerves of the life of relation; in these same segments we no longer find the medullary origins of the corresponding ganglia of the great sympathetic; to meet again with these, it is necessary to seek for them in the segments situated above or below; they are enclosed almost entirely in the segments of the thoracic spinal cord alone.

In reality, these two orders of origin, although both may be medullary, are in no sense equivalent. The condensation of the medullary origins of the great sympathetic in a special region of the grey axis indicates that they correspond in this to a systematization of the second degree, where metamerism has almost disappeared. The graduated arrangement of the motor nuclei of the skeletal muscles implies, on the contrary, a systematization of the first degree, in which metamerism is recognizable. To the system of vegetative life the spinal cord is already what the medulla oblongata, the pons and the cerebral ganglia are to the system of the life of relation. The dissociation in height of the two systems, which is so obvious between their inferior portions, is maintained in the depth of the nervous system.

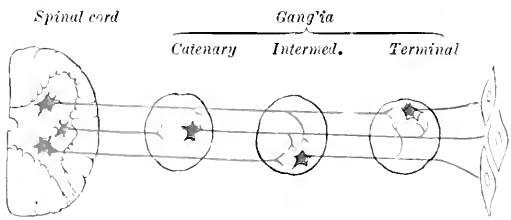


FIG. 131.—Extension of the myelomere outside the vertebral canal (diagram).

Spinal cord, ganglion of the chain, intermediate and terminal ganglia belonging to the same metamere.

Peripheral neurons in blue; deep neurons in red.—Their principal locality of union is in one of the ganglia situated in the course of the nerve.—Collaterals distribute the impulse from one neuron to several ganglia.

Extension of the Spinal Cord up to the limit of the Ganglionic System.—In principle, we maintain that the great sympathetic is formed, in proceeding from the spinal cord to the periphery, by two neurons, placed end to end and united in a ganglion; such is, diagrammetrically represented, its characteristic disposition. Nevertheless, we notice that its branches traverse, not one, but generally three orders of successive ganglia, which may be distinguished topographically in the following manner: (1) the ganglia of the chain (or vertebral), (2) the ganglia of the periphery (terminal ganglionic plexuses), (3) the ganglia occupying an intermediate position (in the same way as the cœliac and mesenteric ganglia). There are reasons for thinking that, as regards

a given fibre, the break is made in one or other of these localities, but not of necessity, and, above all, not totally, in the three successively. The spino-ganglionic neuron has received different but equivalent names (*pre-ganglionic fibre,* fibre of projection of the second order); as also the ganglio-peripheral neuron (*post-ganglionic fibre,* fibre of projection of the first order, etc.).

Long and short paths.—To a greater or lesser degree it is admitted that there is a rough sketch of this kind, which may be compared to that of the voluntary nerves, proceeding from the cortex to the skeletal muscles, by two orders of fibres of projection, united in the grey matter of the spinal cord. On this primitive scheme it is probable that complications are grafted by the addition of commissural inter-ganglionic fibres, comparable to the fibres of association mutually uniting the stages of the cord. Physiologists have denied their existence, but no decisive experiment has been brought forward in disproof of it. As to the intra-ganglionic elements of association, they are evident. The sympathetic would have, then, like the voluntary system, its long and its short paths.

Graduated arrangement of the ganglionic relays.—This graduated arrangement of the grey masses, in which the articulation of the neurons is effected, explains certain apparently contradictory results with regard to the degeneration of the sympathetic nerves. If their medullary roots be cut, these nerves are neither entirely degenerated, as Schiff believed, nor entirely preserved through their ganglia as Waller thought; but the branches of the chain to which they give origin present a mixture of healthy and degenerated fibres, of which some have their trophic centre in the ganglia and others in the spinal cord.

This graduation appears to exist as regards fibres of the same function. If, in the skull, the facial nerve which contains the origin of the vaso-dilators of the tongue be cut, and if, after degeneration, the chorda tympani nerve be stimulated, the vaso-motor excitability of the latter is observed to be diminished, but not wholly abolished (Morat). When the vagus is stimulated in the horse, it sometimes happens that the cardiac muscle is tetanized, as would be the case with an ordinary muscle (Arloing); it is possible that, in this case, the fibres proceeding directly to the myocardium, and not those going to its motor ganglia are acted on.

Lastly, the graduated arrangement of the terminations of the neurons in the ganglia which follow each other must be admitted not only for individually distinct neurons, but for their collaterals, which exhaust themselves the one after the other in these ganglia, before giving their terminal branches to the most remote among them.

Constitution of the Sympathetic Chain.—These ganglia, placed in succession on a conducting path of the great sympathetic, do not exactly form stages, like the superposed segments of the spinal cord, but, on the contrary, *an extension in width* of the myelomere to which they belong. It is quite otherwise with the ganglia of the chain which truly indicate the *metameric superposed stages* of the great sympathetic; each of these stages, in order to perfect itself, adjoining a respective portion of the terminal plexus and of the intermediate ganglia.

As the sympathetic fibres, in order to reach their branches of peripheral distribution, generally pursue a certain vertical course in the

chain, and pass through a certain number of its ganglia, the same question may be proposed concerning them as for those which are situated outside it. Between these ganglia, which are those, or rather which is that forming the point of union between the spino-ganglionic and the ganglio-peripheral neuron? Is it that which is opposite to the nerve pair whence come the fibres starting from the spinal cord? Or, more probably, that which is opposite to the branch of distribution, and which conveys the fibres to the periphery? Langley, who has studied this question in detail, maintains that it is the ganglion opposite to the branch of distribution (it, or one of those which follow it on the branch) which indicates the stage where one of the two neurons ends or the other begins. Starting from the spinal cord, the spino-ganglionic neuron first follows the corresponding root, reaches the chain at the level of a ganglion (or in its neighbourhood), ascends or

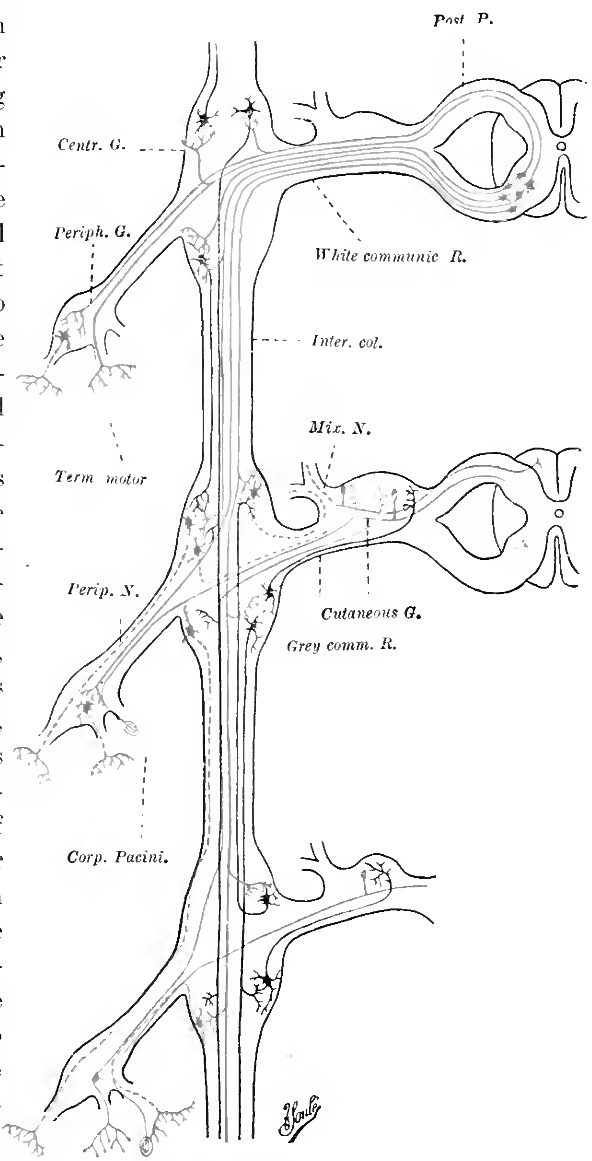


FIG. 132.—Diagrammatic representation of the great sympathetic: structure of the chain (Soulie).

Centripetal neurons in blue; centrifugal neurons in red. In the motor field the deep neurons (medullo-ganglionic) are in red lines; the terminal neurons (ganglio-peripheral) are in red dotted lines; the neurons of association in black.

descends through the length of the latter, passes through one or several ganglia, in one of which it ends. The arborizations there come in contact with the dendrites of one or of several ganglio-peripheral neurons, which leave the chain to go to their destination.

Hence it follows that, of the two neurons which succeed one another in the system of which they form a part, there is only one (the peripheral) which maintains throughout its course the primitive metameric arrangement of the embryo. Its peripheral area, its course, its centre of origin (sympathetic ganglion) occupy the same section as the area of distribution, the course, the centres of origin (spinal ganglion and anterior cornua of the spinal cord) of the nerve pair which it accompanies in its distribution. As to the other neuron, it is, like the cortical medullary neuron of the voluntary system, not included in the primitive metamerism ; like this latter, it forms a new systematization, very different, however, from its own.

The preceding description answers to a general rule, or at least to a more or less marked tendency ; but doubtless there are certain exceptions to this rule.

Cutaneous areas of the Great Sympathetic.—It is by studying the phenomena which depend on the sympathetic, and which are visible at the surface of the skin (condition of the circulation, sudoriparous secretion, and especially movement of the hair), that it has been possible to determine with precision the areas appertaining to each of the ganglia of the sympathetic chain or, which amounts to the same thing, to its branch of distribution. These territories are the same as those of the sensory root which corresponds to this ganglion and to this branch. They differ from them in this, that their limits are more defined and their zones of overlapping less extensive. This concordance is a strong argument in favour of ganglionic metamerism.

SUMMARY.

Unity of plan.—The nervous system of animal life and the nervous system of vegetative life are built up on the same general type ; both are formed of two neurons at least, or of two superposed orders of fibres of projection which come into relationship by their opposed poles, in definite areas of the grey matter.

Two successive neurons.—As regards the nervous system of animal life, these two neurons are, the one *cortico-spinal* and the other *spino-peripheral*. As regards the nervous system of vegetative life, they are, the one spino-ganglionic, the other ganglio-peripheral.

Peripheral and deep System.—From the cerebral cortex to the spinal cord and from the cord to the periphery, as also from the cord to the ganglia and the ganglia to the periphery, double paths exist having an oppo ed conductivity, that is to say, the one *sensory* the other *motor*. Each of the two systems (*animal* and *vegetative*) is thus made up of a *peripheral* and a *deep* system.

Lateral displacement of the Primary Nuclei.—With regard to the osseous case,

formed by the vertebral column, the peripheral system of animal life has its sensori-motor primary nuclei all situated *internally*, while those of the peripheral system of the vegetative life are *external* to this case.

Completed Myelomere.—This dissociation of the primary nuclei permits, nevertheless, the persistence of their primitive metameric disposition, in the sense that those which correspond on transverse planes (the one within the other without the spinal column) may be regarded as forming part of the same *myelomere*, and that their fibres of distribution, mixed in the mixed trunks, proceed to the same *dermatomere*.

Vertical displacement of the secondary nuclei.—On the other hand, the reciprocal displacement of the secondary nuclei (sensori-motor of the deep systems) allows the persistence of scarcely a trace of primitive metamerism, for which it

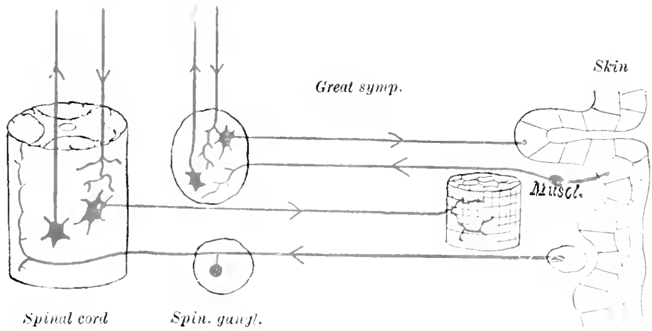


FIG. 133.—Voluntary and involuntary nervous systems.

Diagram pointing out their essential resemblance. Peripheral cycles (metameric) in blue (spinal nerves and branches of the great sympathetic). Deep cycles (not metameric) in red (columns of the spinal cord and of the sympathetic chain). The arrows represent the sensory and motor nerves in the two portions of the two systems.

substitutes a new organization, in which the two systems assume their most pronounced respective characters and their most characteristic differentiation. This displacement is no longer *lateral*, but in the direction of the nerve axis (in the *vertical* direction in man).

The animal system has its superior or deep centres situated in the skull, obviously *above* the primary centres. In the vegetative system the deep centres are in the vertebral column itself (where they there precede its primary or inferior centres) and no longer above, but *within* its strictly primary centres (which are in the ganglia of the great sympathetic), no longer directly opposite to these latter, but on the contrary condensed into certain definite regions of the grey medullary axis (chiefly the *thoracic region*).

Secondary reinforcing nuclei.—The deep nuclei of the great sympathetic are condensed in the thoracic region to such a degree indeed that there are few organs with which this region is not connected by its vegetative nerves (especially the vaso-motors). Nevertheless, these nuclei are found also in two other regions of the grey medullary axis, namely, as regards the inferior portion of the body, in *the lumbo-sacral region*, as regards the superior portion, *the bulbar region*. The nerves taking origin from these localities do not throw themselves into the chain, but sometimes pass it by and proceed to remote ganglia or plexuses (erector, nerves going to the hypogastric plexus; pneumogastric nerve going to cardiac, pulmonary, intestinal plexuses, etc.).

Dissociation of the two Deep or Superior Systems.—The fibres of projection of the second order (fibres of the two deep systems, animal and vegetative) are thus, from this fact, altogether separated. Those of the animal system form

an important portion of the white tracts of the spinal cord ; those of the vegetative system form an equally important part of the cords of the sympathetic chain. The first proceed from the interior of the skull to the interior of the spinal column (or conversely), the second go from the interior of the spinal column to some ganglion external to it (or conversely). The first form a fan or cone with a vertical axis (in man) spread out above ; the second form a fan or cone with a transverse axis expanded outside.

Metamerism and Symmetry.—The two peripheral systems (the animal and the vegetative) still greatly resemble one another, in the sense that they are both metameric (by reproduction of the same parts) and symmetrical (by enlargement of certain of these portions at an equal distance above and below a transverse plane passing through the middle of the spinal cord). The two deep systems are, from these points of view, very different, in the sense that the animal system, in addition to not being metameric, is markedly unsymmetrical ; while the vegetative system, which has equally broken with metamerism, still preserves a symmetrical arrangement in relation to the transverse plane above referred to.

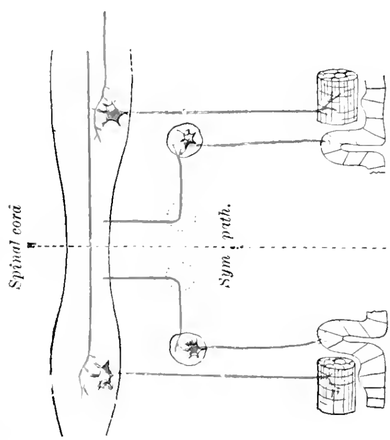


Fig. 134.—Voluntary and involuntary motor systems.

Diagram showing the unsymmetrical arrangement of the deep origins of the first, compared with the symmetrical arrangement of those of the second.

Peripheral neurons (metameric) in blue deep neurons (not metameric) in red.

Approximation of non-equivalent Centres.—The displacements which are thus produced, between the primary centres in the lateral direction, and between the secondary centres in the vertical direction, have produced the effect of bringing both together into the same neighbourhood and of mixing, though partially, in the grey medullary axis, the deep centres of the great sympathetic with the inferior centres of the animal system. It must be remembered that, in spite of their medullary situation and their proximity, they are in no sense equivalent, either as regards order of functions or of centres in the performance of these functions. Although intercalated the one with the other, they are not the less distinct, affecting, when considered separately, a topography which is special to each (reinforcement of the primary centres of the animal life in the cervical and lumbar regions ; coalescence of the deep centres of the vegetative life in the thoracic region). So that, for a given area (dermatomere), *the primary or inferior centres of the animal system will be situated in the corresponding myelomere, while the secondary or deep centres of the vegetative system will be found in a myelomere which is sometimes remote.* It must be added that, *as regards this same given area, the secondary vegetative or deep centres which represent its different vegetative functions* (circulation, etc.) *are intimately mixed in the segments of the grey axis which contain them.*

The Roots ; Selection and mixture according to the order of functions.—For the same reason, the medullary roots, which emerge from the spinal column through the intervals between the vertebrae, also contain mixtures of the primary neurons of the inferior animal system and secondary neurons of the deep vegetative system. As regards the first (animal system), they are distributed, the sensory exclusively in the posterior roots, the motor exclusively in the anterior roots ; as regards the second (vegetative system), this tendency remains, but

there is a mixture of a certain number of motor and sensory fibres (as there is known to be a mixture of the fibres of the two functions in the cortico-spinal tracts of the superior animal system).

The Inter-central elements of inhibition; topographical difference.—The animal and the vegetative system both contain *inhibitory* elements; in both, these elements, formed by *inter-central* neurons, are necessarily limited to the deep or superior system. *The intra-rachidian situation of the primary centres of the animal system causes all these inhibitory elements to take refuge in the cord and the brain: the extra-rachidian situation of the primary centres of the vegetative system causes these inhibitory elements to emerge with the medullary roots and they are observable in them and in the communicating or pre-ganglionic branches of the great sympathetic.*

5. Topographical Determinations

The great sympathetic is distributed partly to the *muscular fibres*, partly to the *glandular cells*, and hence includes *motor* elements strictly so called and *secretory* elements. As regards its functions, this is an elementary and primordial division. Whether muscular or glandular, the elements which it controls appertain to apparatus performing distinct functions (vaso-motor, intestino-motor, sudoriparous, muciparous, lactiferous, etc.). This is still a functional division, but a secondary one. Whether primitive or secondary, these functions are nevertheless external to itself. With regard to the mutual internal relations of its elements, we divide them into *immediate* and *mediate*, or those of the first or second degree; or, again, into infra-ganglionic and supra-ganglionic, in other words, infracentral and intercentral; and in this second category (intercentral elements), we distinguish *excito-motor* and *excito-inhibitory* elements; or, again, those with a positive and those with a negative action.

Its arrangement, approximately regular, furnishes us also with another division of a purely topographical order. With regard to the layers of the blastoderm, its branches of distribution, starting from the chain, are on the one hand *visceral* and on the other *cutaneous* or, in other words, direct (proceeding to their termination without union with other nerves), and indirect (mixing in the mixed trunks with nerves of function of a voluntary conscious order). With regard to the axis of the body, considering it apart from its medullary origins, we find it affecting further characteristic arrangements.

Taking origin principally in the thoracic spinal cord, its branches again join the chain, and thence, by a double symmetrical extension above and below, are distributed to all parts of the body (after section in the ganglia, both of the chain and of the trunks given off from it). Both above and below, they meet with (by the chain or without the chain) reinforcing elements, supplied by the bulbar and the sacral

region. As regards a plane which cuts the body transversely at the level of the eighth or ninth thoracic vertebræ, there is thus a superior *and an inferior half* of the great sympathetic, which are repeated with a certain symmetry.

A. SUPERIOR HALF.—This portion of the great sympathetic receives

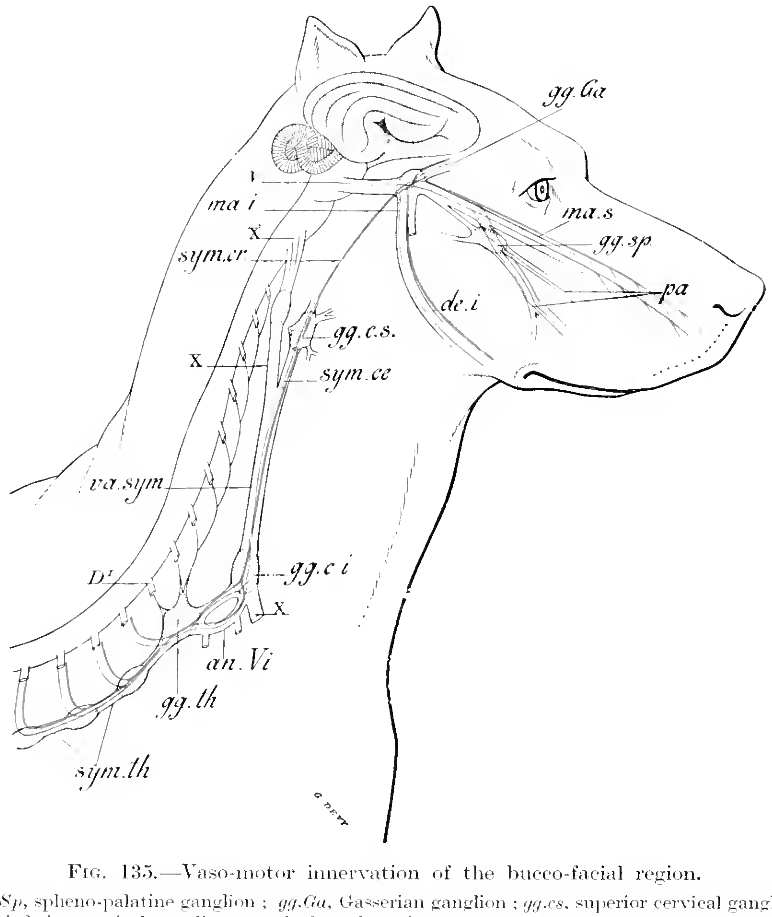


FIG. 135.—Vaso-motor innervation of the bucco-facial region.

gg.Sp, spheno-palatine ganglion; *gg.Ga*, Gasserian ganglion; *gg.cs*, superior cervical ganglion; *gg.ci*, inferior cervical ganglion; *gg.th*, first thoracic ganglion; *ma.s*, superior maxillary nerve; *pa*, palatine nerves; *ma.i*, inferior maxillary nerve; *de.i*, inferior dental nerve; *sym.ce*, cervical sympathetic; *sym.cr*, its cranial prolongation going to the Gasserian ganglion; *va.sym*, common trunk of the vagus and the sympathetic; *an.Vi*, ansa Vieussenii; *sym.th*, thoracic sympathetic with its original communicating branches of the dorsal pairs; V, origin of the trigeminal; D1, first dorsal pair (constrictor filaments in blue, dilator in red).

its spino-ganglionic elements, partly from the spinal cord, partly from the medulla oblongata.

1. **Elements of medullary origin.**—The superior half of the thoracic cord supplies origins which, by the sympathetic chain, terminate generally in the ganglia of the base of the neck (middle and inferior

cervical in man, inferior cervical and first thoracic in animals). In proceeding from one to the other of these two ganglia, the chain breaks up, embraces the sub-clavian artery, and thus constitutes what is known as the *Ansa Vieussenii*. The whole of this region gives off, in two principal directions, two important branches which proceed, some to the thoracic viscera, others to the superior extremity. Re-organized, the chain, under the name of *cervical cord,* traverses the whole length of the great vessels of the neck, passes once again through a large ganglion (superior cervical ganglion); then, from the superior extremity of the latter, it proceeds to the Gasserian ganglion of the trigeminal, by the branch of which it reaches the ophthalmic, sphenopalatine and otic ganglia. The anastomosis between the superior cervical ganglion and the trigeminal may be regarded as the prolongation of the chain, the *cranial cord* of the great sympathetic (Morat).

The Ansa Vieussenii is a sort of nodal point, starting from which the distribution of the sympathetic takes three directions through three groups of fibres, one for the head, one for the superior limb, one for the viscera of the chest. From a purely descriptive point of view, this latter group is direct, which merely implies that it forms no anastomosis with the mixed nerves of the spinal pairs; the two others are indirect, meaning that their elements, emerging from the chain, follow (with the exception of some fibres proceeding by the path of the arteries to the anterior and posterior brain) the path of the mixed bulbo-medullary trunks, those of the brachial plexus for the superior limb, those of the trigeminal for the face.

First Group: Sympathetic innervation of the head and neck.—All the organs of the head, including the brain, receive, by this route, a motor influence which comes to them from the thoracic spinal cord and which controls the functions of involuntary movement represented in it. This is well seen when the sympathetic is cut or stimulated at any point in this long course. These perturbations may indeed be classed as ŏculo-pupillary, vaso-motor and secretory.

Oculo-pupillary effects.—When the great sympathetic is stimulated, the eye protrudes and separates the eyelids (by contraction of the smooth muscular fibres of the capsule of Tenon and also of those which are contained in the eyelids); the pupil dilates, either by inhibition of the motor forces which contract the iris, or by stimulation of a muscle having a radiating action (muscular layer of Grynfeld).

The lens is also flattened, either by inhibition of the ciliary muscle, or by stimulation of an antagonistic muscle which may also exist.

Vaso-motor effects.—They are of two kinds; stimulation has *vaso-constrictor or vaso-dilator* effects according to the locality under observation, the animal operated on, and the region in which the great sympathetic is stimulated. In

the dog the following division is observed. Apart from stimulation of the great sympathetic in the neck, constriction of the vessels of the conjunctivæ, of the iris, of the ear, of the tongue, of the epiglottis, of the tonsil, of the soft palate is caused ; and, on the other hand, congestive dilatation of the vessels of the retina, of the lips, of the gums, of the cheeks, of the palatine arch, of the nose (skin and mucous membrane), of the tongue, of the salivary glands. Stimulation of the great sympathetic acts further (according to circumstances, in one or the other senses indicated) on the circulation of the brain and on that of the thyroid gland. On opening one of the efferent vessels of a lymphatic gland of the neck, I have observed *the flow of lymph to be considerably increased during stimulation.* Whatever opinion may be held concerning the action (direct or indirect) of the nervous system on the lymphatic apparatus, it is obvious that the great sympathetic regulates the local circulation of this system, as it regulates that of the vascular apparatus. The *thyroid gland* receives its vaso-motor nerves from the superior portion of the thoracic chain by the cervical cord. Stimula-

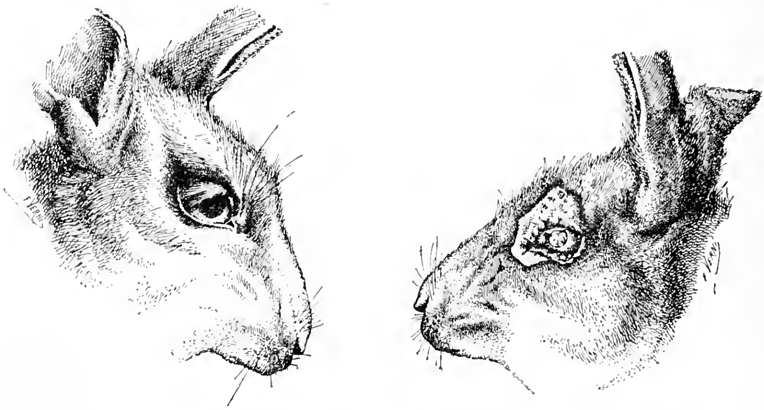


FIG. 136.—Trophic disturbances after section of the cervical sympathetic (Morat and Doyon).

On the left, head of rabbit, normal appearance. On the right, inflammation of the conjunctiva and opacity of the crystalline lens.

tion of the thoracic chain causes either vaso-constriction or vaso-dilatation, on account of the mixture of the two orders of fibres (Morat and Briau).

Secretory effects.—Stimulation of the great sympathetic gives rise to secretion of the sudoriparous glands of the face (clearly visible only in certain animals), that of the lachrymal gland, and that of the submaxillary gland (which under this influence secretes a thick and viscous saliva differing from that which follows stimulation of the chorda tympani). This stimulation modifies the intraocular tension (probably by acting on the internal secretion of the humours of the eye at the same time as on its internal circulation). Section of the cervical sympathetic causes a hypersecretion of the sweat glands, of the Meibomian glands, of the conjunctiva and of the sebaceous glands of the lobe of the ear, phenomena which have not a very definite counterpart in the effects of stimulation, but which are in favour of an inhibitory action attributable to certain fibres contained in the divided nerve trunk.

Trophic effects.—Alongside of these secretory modifications, we must point out once again as distinct phenomena, though fundamentally of the same category, disturbances of epithelial desquamation (Arloing), cutaneous ulcerations, opacities of the lens (Morat and Doyon), all of which have been observed to follow

section of the sympathetic, as results not absolutely invariable but fairly frequent. These disturbances, known as *trophic*, should be regarded as a secondary more or less remote effect of the functional disturbance resulting from defective innervation of the tissues in which they are observed.

In order to increase these trophic effects of paralysis of the sympathetic, Angelluci has practised removal of the superior cervical ganglion on newly born animals, and has observed as the result of this operation disturbance of *development* of the face, of the skull and of the ball of the eye, and alterations of their different tissues. These disturbances, varying according to the animal, are more marked in the dog. The author has noted an alopecia of the face, a dystrophy of the bones of the skull, a vicious development of the teeth, a reduction in the dimensions of the cornea and of the sclerotic: the ball of the eye has shrunk about a millimetre in diameter. There is at the same time simple atrophy and sclerosis of the iris and of the choroid. The structure of the retina is preserved, and sight is not weakened. The vessels present dilatations and their lumen is narrowed in places. The endocular tension was not diminished, or, if so, has been quickly recovered.

According to Floresco, these effects are only obtained by the section of a considerable length of the nerve or by the ablation of its ganglia (both conditions hindering regeneration). The skin, the muscles, and the eye, undergo an arrest of development. The thyroid gland and the suprarenal capsules become slightly hypertrophied.

Paradoxical motor effect; so-called pseudo-motor influence.—When the hypoglossal nerve has been cut on its course, its peripheral end, or the one which proceeds to the tongue, degenerates conformably to the well-known law of Waller; it consequently becomes inexcitable after two or three days. If the chorda tympani of the same side be exposed, and it be cut and its peripheral end stimulated, a new phenomenon arises which is absolutely inexplicable in the present state of our knowledge. *This stimulation, which ordinarily only acts on the vessels of the tongue by causing them to dilate, gives rise to contractions of the lingual muscles themselves* (Philippeaux and Vulpian).

These contractions are much feebler than those excited by the hypoglossal; they are most obvious towards the fourteenth day after section; their latent period is much longer; their form is much shorter, and they can scarcely be rendered evident except by a series of shocks producing their summation. While the hypoglossal is excitable by salt water, the chorda tympani (or the lingual which contains it) is not excited. Nicotine, which does not act on the hypoglossal, excites these new contractions when it is injected into the blood (Heidenhain). The paradox consists in this: a nerve which was not a motor nerve of the tongue, has become motor for its intrinsic muscles after section of the hypoglossal. This nerve comports itself as a nerve of organic life. Further, the phenomenon is independent of the circulation; it occurs when the tongue with its nerve trunks is detached from the animal (Morat).

Rogowics has observed that, after section of the facial nerve, the cervical great sympathetic also assumes this singular property as regards the nerves of the lip. This *pseudo-motricity* appears to be peculiar to the *vaso-dilatory* nerves.

2. **Elements supplied by the Bulb.**—The sympathetic elements, which from the thoracic cord are distributed to the head, are there reinforced by other identical functional elements contained in the origins of the cranial nerves, as are the preceding in the origins of the thoracic nerves. The *trigeminal* supplies oculo-pupillary nerves (dilator of the iris and accommodator for distant vision), a nerve for the middle ear (to the

internal muscle of the malleus or tensor tympani). The sympathetic nature of this nerve filament is proved by the presence in the dog of a very obvious ganglion at a point where the nerve penetrates the muscle. The trigeminal supplies vaso-motor nerves (dilators for the retina and the face) ; it supplies secretory nerves (for the lachrymal gland, etc.) which go to rejoin the preceding in the Gasserian ganglian.

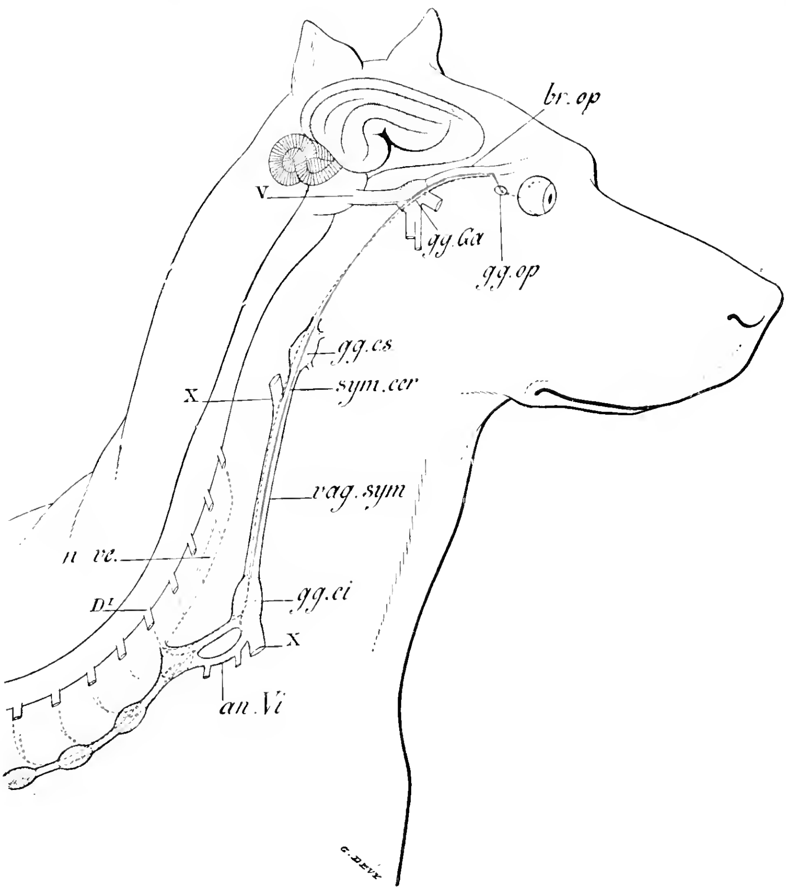


Fig. 137.—Vaso-motor innervation of the retina.

gg.op, ophthalmic ganglion ; *gg.Ga*, Gasserian ganglion ; *gg.c.s*, superior cervical ganglion ; *n.ci*, ciliary nerves ; *br.op*, ophthalmic branch of Willis ; *symp.cr*, cranial prolongation of the sympathetic ; *symp.cer*, cervical sympathetic ; *vag.symp*, common trunk of the vagus and of the sympathetic ; *V*, origin of the trigeminal ; *D'*, origin of the first dorsal pair ; *an.Vi*, ansa Vieussenii ; *n.ve*, vertebral nerve (constrictors in blue, dilators in red).

The *oculo-motor* nerve supplies oculo-pupillary nerves (constrictors for the sphincter of the iris and for accommodation for near vision).

The *facial* nerve supplies vaso-dilator nerves for the soft palate (great petrosal and posterior palatine nerves), branches for the tongue and the submaxillary and sublingual glands (chorda tympani) ; it supplies

secretory nerves for the soft palate and the submaxillary and the sub-lingual glands following the same course as the preceding (the saliva whose secretion is excited by stimulation of the chorda tympani is watery and limpid compared to that secreted by stimulation of the cervical sympathetic). This same nerve gives a filament for the muscle of the stapes, whose action is antagonistic to that of the internal muscle of the malleus.

The *glosso-pharyngeal* supplies vaso-dilator branches to the posterior

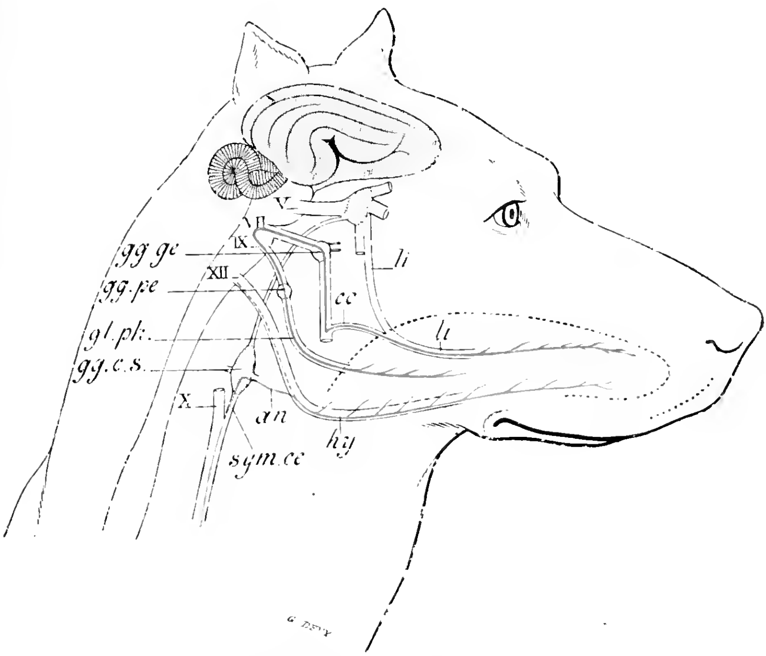


FIG. 138.—Vaso-motor innervation of the tongue.

gg.ge, geniculate ganglion of the facial (VII); *gg.pe*, petrosal ganglion of the glosso-pharyngeal (*gl.ph*); *gg.c.s*, superior cervical sympathetic ganglion; *sym.cc*, cervical sympathetic; *an*, anastomosis of the superior cervical ganglion with the hypoglossal (*hy*); *li*, lingual; *c.o*, chorda tympani (constrictor nerves in blue, dilators in red).

portion of the tongue, vaso-dilator and secretory elements to the parotid gland (small deep external petrosal proceeding from the jugular ganglion of the glosso-pharyngeal to the otic ganglion).

The *vagus* supplies vaso-dilatory and secretory elements to the larynx by the laryngeal nerves.

Remark.—The neurons proceeding from the medulla oblongata which are thus united to the great sympathetic by the aid of the cranial ganglia of the latter, are fibres of projection of the second order, supra-ganglionic, intercentral. It should be noted that a considerable portion of these neurons follow sensory nerve trunks (especially the trigeminal);

they are the equivalents of the sympathetic elements which leave the cord by the posterior spinal roots at the level of the plexuses of the extremities ; they resemble them in this that, on the one hand they are, although centrifugal, mixed with sensory fibres ; and on the other, that they take their origins in the grey axis at the same level as the nerves discharging sensory functions in the regions to which they are distributed.

Another portion of these reinforcing elements, that which is represented by the facial, the glosso-pharyngeal, and the vagus, has a further characteristic : that, namely, of avoiding the sympathetic chain itself,

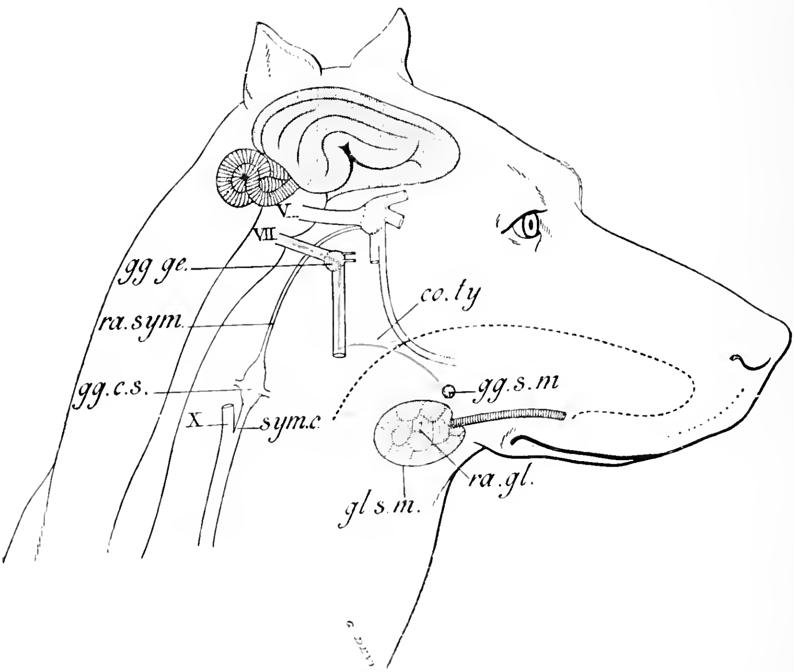


FIG. 139.—Vaso-motor innervation of the sub-maxillary gland.

gl.s.m, sub-maxillary gland and its excretory duct ; *gg.s.m*, sub-maxillary gland ; *gg.c.s*, superior cervical ganglion ; *gg.ge*, geniculate ganglion ; *ra.gl*, intraglandular ramifications ; *ra.sym*, cranial sympathetic ; *sym.c*, cervical sympathetic ; *co.ty*, chorda tympani ; VII, facial (constrictors in blue, dilators in red).

and of rejoining the sympathetic elements in the remote or terminal ganglia. We shall encounter an arrangement of the same kind in the inferior half of the great sympathetic ; it is that of the erector nerves which, starting from the sacral cord, cross the chain without entering it and lose themselves in the hypogastric plexus.

Second Group : sympathetic nerves of the superior limb.—They have nearly the same medullary origin as those of the head. Their

ganglionic origin is indicated by the stellate or first thoracic ganglion; from this ganglion they pass through the vertebral nerve (and also through the subjacent communicating branch) in order to rejoin the brachial plexus.

Vertebral Nerve.—The condensation of the ganglia of the inferior cervical and superior thoracic region into a single mass (stellate ganglion) necessitates the condensation of the communicating branches which correspond to it into a single nerve trunk, the vertebral nerve. Starting from this ganglion, the nerve re-ascends, crossing over the origins of the brachial plexus, and gives to each of them a filament representing its communicating branch. The name *vertebral*, given to this nerve, is due to its situation and to its course in the costo-transverse foramina of the cervical vertebræ, throughout the length of the vertebral artery, which it accompanies and to which it supplies ramifications, as also to its branches and terminations.

The vertebral nerve is formed for the greater part by grey non-myelinated fibres, which, functionally, are fibres of distribution (efferent), in other words, fibres (motor) of projection of the first order. Of these fibres some throw themselves directly on the vertebral artery, thus corresponding to the *direct* or visceral arteries properly so called, which, from the ganglia of the chain, proceed to the larger viscera; the others attach themselves to the branches of distribution of the brachial plexus, thus corresponding to the *indirect* branches which go to the vessels and the glands of the skin by way of the cutaneous nerves. These last are a mixture of vaso-motor, secretory and pilo-motor elements intended for the corresponding apparatus which is situated in the skin and also for the vessels of the muscles of that area.

Whether direct or indirect, these nerve branches are a mixture of elements, the one excitatory and the other inhibitory for corresponding functions. As regards vaso-motor function, they contain constrictors and dilators of the vessels: this is proved experimentally by the production of local changes in the circulation in the corresponding limb and in the vertebral artery (François-Franck).

The spinal origins of the vertebral nerve are situated in the thoracic roots, from the second to about the sixth or eighth. Having left the cord by the corresponding roots and communicating branches, they ascend the thoracic chain of the sympathetic and become articulated (partially at least) in the stellate ganglion with the fibres of distribution. They are motor neurons of the second order, just as the preceding are the motor neurons of the first order. In somewhat the same way the thoracic nerves *give* off fibres which (after or without interruption) are *received* by the cervical nerves of the brachial plexus in order to proceed with it to the periphery. Do the roots of the brachial plexus do the same in the opposite sense? Do they give motor fibres to the vertebral nerve and to the sympathetic chain which the latter afterwards distribute? If this is so the number thereof is very limited.

Sensory fibres.—The origins of the brachial plexus thus contain few or no centrifugal fibres of sympathetic nature; but, according to François-Franck, they contain *centripetal* or sensory fibres conveying impressions coming from the viscera, which, following the sympathetic chain and the vertebral nerve, penetrate into the spinal cord, whence they are capable of reacting in the form of generalized reflex vaso-motor effects, manifesting themselves as defensive reactions, therefore as manifestations of conscious sensibility. According to François-Franck, these effects would not be the consequence of arterial spasm of the vertebral artery and of the cerebral anæmia, which is the consequence of it, but a direct sensory effect.

Third Group: visceral thoracic nerves.——From the ganglia of the base of the neck (inferior cervical and first thoracic in animals) and from the Ansa Vieussenii, fibres arise which proceed to the ganglia of the heart and to the ganglia (plexiform) of the lung. Those which go to the heart are *accelerators* of its movements. Their stimulation has not the tetanizing effect of that of ordinary motor nerves; they do not proceed strictly to the heart muscle, but to its motor ganglia, whose special action they stimulate. To these ganglia other fibres also proceed which have taken origin in the pneumogastric, and which exert on them, and therefore on the heart, an inhibitory influence. They clearly enter into the formation of the great sympathetic system, of which they are aberrant elements; they are further mixed with some accelerating fibres having the same origin.

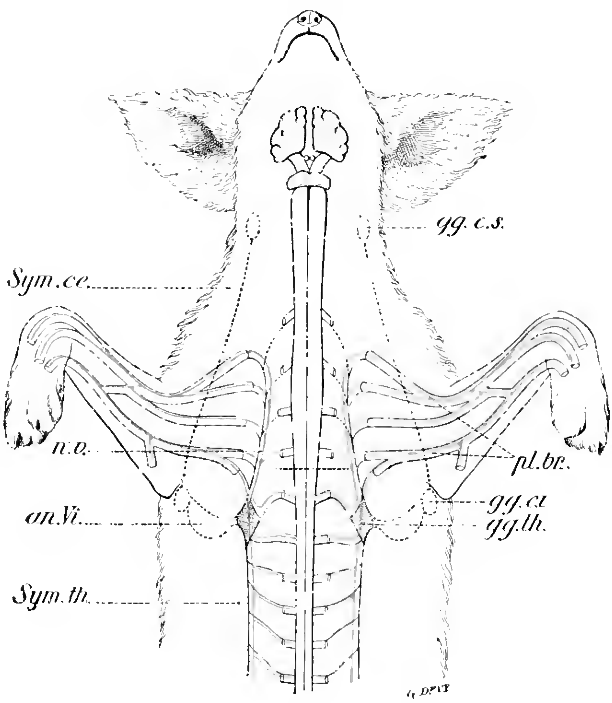


FIG. 140.—Medullary origin and distribution of the ganglionic motor nerves of the thoracic limb.

Vaso-motor nerves in red; sweat nerves in yellow.
The branches of origin are furnished by the thoracic spinal cord and follow the chain; the branches of distribution follow the vertebral nerve *nv*, in order to join the brachial plexus.

Like the ganglia of the heart, the pulmonary plexus receives fibres both from the great sympathetic and the pneumogastric. The functions to be fulfilled are here more numerous, the lung possessing, in addition to its intrinsic muscles, vessels and glands. The bronchial muscles may be stimulated and also inhibited by elements coming from the pneumogastric. The pulmonary vessels receive constrictors coming from the great sympathetic; the innervation of the glands is imperfectly known.

B. Inferior Half.—From the inferior portions of the thoracic and superior portions of the lumbar cord fibres proceed by communicating branches, which rejoin the lumbar chain ; they follow this chain in a descending direction as far as the caudal extremity, where they terminate. These are the diminished equivalent of the group which in the superior half goes to the head. In the locality where the chain crosses the lumbo-sacral plexus, it provides it with branches of distribution going to the inferior limb ; this is the repetition of what we have already seen in the brachial plexus. Finally, from a large extent of the dorsal, andfrom the superior part of the lumbar spinal cord, important branches are detached, which go to the abdominal viscera : this is a third group and comprises direct or visceral elements properly so called. As for the origins and strengthening elements, they also are not lacking here : we find them in the lumbo-sacral spinal cord, furnishing them directly to the sacral plexus which supplies, in addition, the erector nerves terminating in the hypogastric plexus.

First or Caudal Group.—This is represented by a few vaso-motor, pilo-motor, and secretory elements, for the vessels, the hairs and the glands of the skin.

The tail in animals forms a series of metameres (but not very recognizable) which prolong those of the trunk (the limits of the latter being distinctly fixed). On the contrary, to the whole length of the latter, to each ganglion, a cutaneous area corresponds.

Sympathetic nerves of the trunk.—If we take the trunk as a whole, we see that to each ganglion a series of spinal origins correspond which are only exceptionally on the same level as themselves. The portrayal of these correspondences, which is too long to describe, will be more easily represented by a diagram. The diagram may be specially based on indications furnished by erection of the fur when the pre- and post-ganglionic branches of the sympathetic chain are stimulated.

It must not be forgotten that the first thoracic or stellate ganglion corresponds, not only to the inferior cervical region, but also to the commencement of the thoracic region. Thus, it is more especially in the inferior half of the body that the metameric ganglionic arrangement pointed out above is once more met with.

Second Group, or that of the Lower Limb.—This has its orgins in the spinal cord, from the tenth or eleventh dorsal as far as the second lumbar. It contains, like the preceding, *vaso-motor*, *pilo-motor* and *secretory* (sudoriparous and sebaceous) elements. Here the vaso-motor elements are some *constrictors*, and others *dilators* of the vessels ; sometimes one, and sometimes the other, are more easily demonstrable.

Experiment.—If the dorsal sympathetic chain be stimulated immediately above the diaphragm, the arterial pressure is seen to be locally raised in the corresponding inferior limb, this being due to the fact of the equally localized

constriction of most of the vessels of this limb: this proves the existence of constrictor nervous elements. At the same moment the skin, and especially the digital pulp, will be observed to be markedly reddened by the afflux of blood: this is proof of the existence of dilator elements for the cutaneous covering. If the stimulation is brought to bear on the lumbar chain, and especially on the trunk of the sciatic nerve, the constrictive effect with regard to the deep vessels remains quite as distinct, but the dilator cutaneous effect becomes inconstant. Stimulation of the sciatic nerve in the cat always produces pallor of the integument (Dastre and Morat). These excitations both of the dorso-lumbar chain and of the sciatic nerve, which receives its fibres of distribution, produce secretion of the cutaneous sudoriparous glands (Luchsinger).

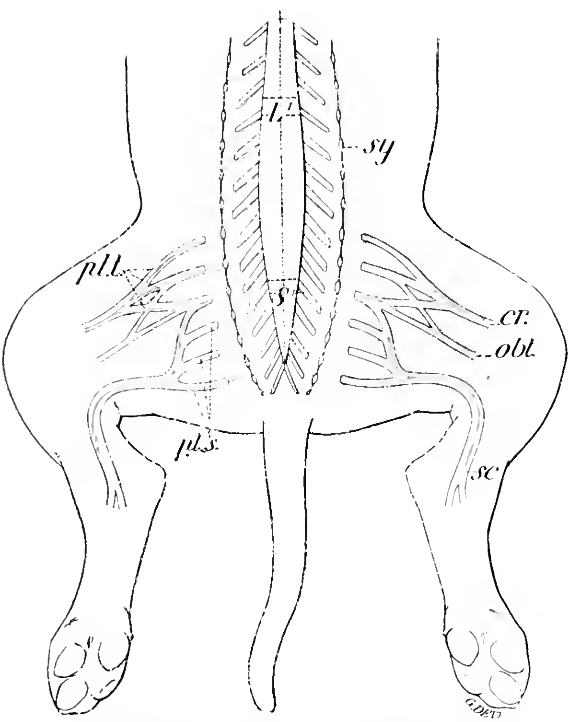


FIG. 141.—Medullary origin and distribution of the ganglionic motor nerves of the abdominal limb.

Vaso-motor nerves in red; sudoriparous nerves in yellow. With some few variations, the origins and the distribution of the involuntary nerves of different functions are practically the same.

These elements of dorso-lumbar origin are reinforced by other arising from the sacral spinal cord, and consequently mixed with the origins of the sacral plexus. The secretory fibres having this origin leave by the anterior roots of the sciatic nerve. The vaso-motor fibres emerge with the *posterior roots*, and are exclusively *vaso-dilator*. There are no pilo-motor fibres having this origin.

Third Group, or that of the Abdominal Viscera.—This is highly important, on account of the large number of organs to which its branches of distribution repair. In order to construct a natural group, its origins must be started from a point a little above that used to divide the great sympathetic into its two halves.

Elements of spinal origin.—This group arises, throughout a great length, from the thoracic spinal cord, and also from the superior portion of the lumbar region of the same. Its origins, after having come into contact with the chain, leave it under the form of trunks more or less condensed, namely, the *splanchnic nerves*, large and small, which

from the chain run to the *coeliac ganglion,* to the *solar plexus* and to the *renal plexus ;* the *mesenteric* nerves, which from the chain end in the superior *mesenteric* ganglion, and after having passed through it proceed to the hypogastric plexus.

Elements of bulbar and sacral origin.—The coeliac, superior mesenteric and hypogastric ganglia are mutually united by links parallel to the sympathetic chain. These ganglia form, in a way, a second chain, anterior to that following the lumbar column. For this reason it is sometimes called the *pre-vertebral chain,* in contrast to the chain properly so-called, which is named *vertebral* (Langley). This second chain receives strengthening elements by two very remarkable paths : the first is that of the *pneumogastric,* which brings it the *bulbar* influence ; the second is constituted by the *erector nerves,* which convey to it the influence of the *sacral* region.

The *pneumogastric* gives off on each side (but especially on the right) an anastomatic branch to the *coeliac ganglion*, and by it enters the solar plexus and extends perhaps as far as the pelvis. The *sacral nerves* cross the vertebral ganglionic chain and throw themselves into the *hypogastric plexus.* Once more we find a kind of symmetrical arrangement above and below, and this may be pointed out as characteristic of the vegetative nervous system. It must be noted that this symmetry has nothing geometrical about it. The bulbar influence has, in comparison with that of the sacral nerves, an extremely extensive field of action. From this fact the vegetative nervous system at this stage displays a tendency to polar dyssymmetry, which, in the animal nervous system, becomes emphasized in the highest degree by the development of the brain.

Abdominal viscera and those of the pelvis : Corresponding nervous groups.—The group of abdominal viscera may itself be divided into two regions : the one abdominal properly so called, comprising the stomach, the small intestine, the liver, the pancreas, the spleen and also the kidney at its boundary ; the other filling the pelvis comprehends the bladder, the rectum, the anus, and the genital organs. To these two visceral regions, nervous trunks and distinct ganglionic plexuses correspond. Connected with the first are the splanchnic nerves, which pass into the coeliac ganglion and the solar plexus, before arriving at their destination in the viscera ; and with the second the mesenteric nerves which, after having passed through the ganglion or mesenteric plexus, fall into the hypogastric plexus, before reaching their visceral terminations. The coeliac plexus, as has just been remarked, receives from the pneumogastric elements which are in general antagonistic to those of the splanchnic, with which, however, they are connected in this ganglion. The hypogastric plexus receives elements from the sacral pair (erector nerves), also in general antagonistic to the mesenteric nerves, but connected with them in this plexus. These two systematic groups are, however, not isolated, but attached to each other by connecting links as well as to the organs which are innervated by them. From a functional point of view they present, in spite of being grouped together, a certain difference which

separates them, and in the same grouping a certain conformity which draws them together. In the superior group the functions are durable or continuously rhythmical; in the inferior they are widely intermittent, as indeed is appropriate for reservoirs which preserve contents eventually to be expelled.

Functional antagonism between elements of different origin.—The special convergence of the branches of the pneumogastric and of the sympathetic on the visceral ganglia has been already pointed out with regard to the heart and the lung in the superior half. It is functionally remarkable on account of the fact of an *antagonistic* action being exercised by these two nerves on these ganglia, or at any rate on the organs depending on them. For the cardiac muscle the pneumogastric is the moderator, and the sympathetic the accelerator of the movements. As concerns the gastric muscles (and also, but less evidently, the

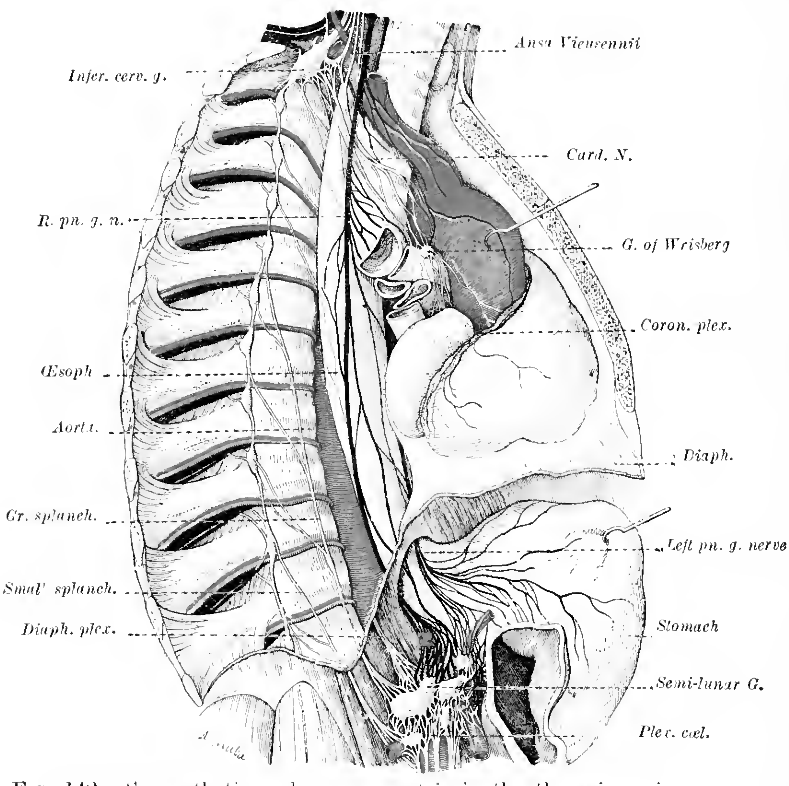


FIG. 142.—Sympathetic and pneumogastric in the thoracic region. Cardiac nerves and splanchnic nerves.

intestinal), the pneumogastric augments and the sympathetic inhibits their tonic or peristaltic contraction. *From one organ to another this antagonism is again met with, but the characters are inverted.* From this it may be seen that one function alone, whether it be motor or inhibitory, is not attached to either one or another of these groups, any more than to the grey nuclei whence they arise. However, it is demonstrable that some of these nerve trunks contain elements fulfilling both functions, and in this case action in one or the other sense results simply from the predominance of either motors or inhibitors according to circumstances.

Innervation of the digestive tube.—The digestive tube is innervated from the pharynx (and even the mouth, as concerns its vessels and glands) by the branches of the great sympathetic and equivalent nerves. Like that of the skin, this innervation answers to three orders of functions (motor, vaso-motor and secretory). The great sympathetic furnishes secretory and vaso-motor fibres to the salivary glands, in concurrence with the nerves of bulbar origin.

Many authors have endeavoured to define the numbers of origin of the spinal nerve pairs which furnish the nervous elements proceeding to the different segments of the digestive tube and its appendant glands. They are unanimous with regard to those of these nerve pairs which represent the principal origins of the elements destined for these viscera. This unanimity ceases when it becomes a question of exactly defining, either above or below, the medullary territory corresponding to these origins; some increasing and others diminishing its extent, either in one or the other direction. This arises from the fact that the medullary territory, more condensed in its medium or cenrtral portion, becomes diffused and lacks clearly defined limits towards its extremities. These divergent results may be explained by individual anatomical differences, or by differences of excitability in these elements reduced to mere traces; or, finally, by variations in the delicacy of the methods of observation made use of.

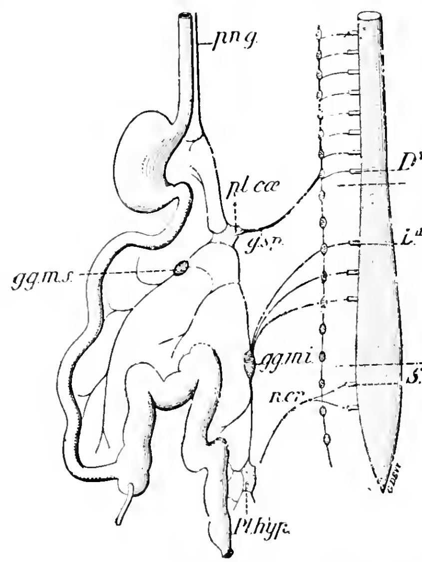


FIG. 143.—Innervation of the intestine in the dog.

pn.g, pneumogastric; *pl.cœ*, cœliac plexus; *gg.m.s*, superior mesenteric ganglion; *gg. m.i*, inferior mesenteric ganglion; *Pl.hyp*, hypogastric plexus; *g.sp*, great splanchnic; *n.er*, erector nerve; DXIII, thirteenth dorsal pair; LIII, third lumbar pair; SI, first sacral pair.

The *œsophagus* receives its motor nerves principally from the pneumogastric. This channel in the dog receives an important branch of the superior cervical ganglion of the great sympathetic, as Espezel has noticed. Here is a new proof of the community of nature of these two nerves.

The *stomach* receives nerves both from the vagus (motor) and from the splanchnics (inhibitory); the origins of these latter extend from the fifth to the eighth thoracic vertebræ.

The *intestine* is also innervated (at least as regards its superior portion) by the vagus (motor) and by the splanchnics (inhibitory) concurrently.

The stomach and the intestine receive their vaso-motor nerves from the two above-mentioned nerve trunks. As regards the intestine, the origins of these nerves extend from the fifth thoracic as far as the second lumbar. The eleventh, twelfth and thirteenth thoracic nerves, as well as the two first lumbar, contain dilators mixed with the constrictors. As ganglionic nerves of different functions have obviously the same origins, we can make use of these determinations to fix the sources of origin of the nervous system, as well for the stomach as for the intestine.

In principle it may also be admitted that the secretory nerves arise from the

same regions at the same time as from the vagus, but the study of these nerves is far less advanced.

The *pancreas* also receive a double innervation from the pneumogastric and from the great sympathetic. For it also branches are detached from the spinal cord, from the fifth or sixth thoracic to the second lumbar. Its vaso-dilators reach it principally from the vagus; there are a very small number of them in those branches of the great sympathetic which are destined for it. Stimulation of the sympathetic origins gives rise more especially to vascular constriction, and only secondarily to dilatation (François-Franck and Hallion). The pancreas receives its secretory nerves from the vagus (Pawlow, Morat). Stimulation of the branches of the sympathetic simultaneously with that of the vagus diminishes and arrests the effects of the latter, by means of a mechanism which is probably one of inhibition (Morat).

The *liver* receives its nerves from the great sympathetic, from the same region of the spinal cord, extending from the sixth thoracic to the second lumbar. This result has been arrived at by observing the vaso-constrictor effects caused by stimulation of the origins of these nerves in the communicating branches. By directly stimulating the nerves of the liver or the large trunks (splanchnic) which furnish them, its circulation and its proper function are both simultaneously acted on; the excretion is modified, if not the biliary secretion. The large splanchnics are the motor nerves of the biliary ducts. An inhibitory apparatus co-exists, which can only be brought into play experimentally by reflex stimulation acting on its central end. Stimulation of the central end of the vagus generally provokes dilatation of the sphincter choledochus in a manner parallel to the contraction of the gall bladder (Doyon).

Stimulation of the splanchnics obviously acts on the glycogenic function of the liver, which is excited by it. An increased activity in the transformation of glycogen into glucose has been observed; this action appears to be independent of the state of the circulation; it would tend to prove the existence of strictly secretory or glucose-forming nerves (Morat and Dufourt).

The *spleen* receives, by the splanchnic, nerves coming to it from the spinal cord, from the third or fourth dorsal as far as the first lumbar (Schaffer and Moore).

The *colon* receives filaments of distribution from the mesenteric nerves arising from the first lumbar pair, almost up to the sixth.

The *rectum* and the *anus* receive elements of similar origin which, descending by the mesenteric nerves, rejoin the hypogastric plexus, where they are duplicated by those provided by the second and third sacral pairs. The anus also receives filaments of sacral production, which reach it directly by the hæmorrhoidal or anal nerve.

Innervation of the urinary apparatus.—The *kidney* (chiefly by the small splanchnic nerves) receives nerves from the great sympathetic, some vaso-motor, others probably exerting a directly stimulating action on secretion. The vaso-motor effects induced by stimulation of these nerves can be readily demonstrated. They take origin more especially from the twelfth and thirteenth thoracic roots Bradford).

The innervation of the *bladder* is almost the same as that of the rectum. Like the latter, it receives filaments from the hypogastric plexus, which itself derives them from a double source, lumbar and sacral. The nerves of the fundus and of the neck of the bladder are antagonistic to one another, being motor for the one and inhibitory for the other; their separation at their bulbar and sacral origins is in no sense absolute.

Innervation of the genital apparatus.—The genital apparatus is composed of reservoirs (in the male vesiculæ seminales, in the female the uterus) and of erec-

tile organs (corpora cavernosa, clitoris). The first are motor and the second vascular structures. Both are lined with secretory organs.

Turgescence of the *erectile structures* is induced by stimulation of the erector nerves of Eckhard (second and third sacral pair), their flaccidity by that of the mesenteric nerves. But these latter also contain dilator elements (François-Franck) and, conversely, some at least of the sacral roots (the second) contain constrictor elements (Nicolsky). The internal pudic nerve also contains elements belonging to both of these orders (François-Franck).

Contraction of the *vesiculæ seminales* with expulsion of their contents is provoked by stimulation of the mesenteric nerves (Loeb, Remy). The contractions of the uterus are under the control of the same nerves. The special action of the sacral nerves upon these organs is unknown. Stimulation of the lumbar sympathetic gives rise to simultaneous contraction of the uterine vessels.

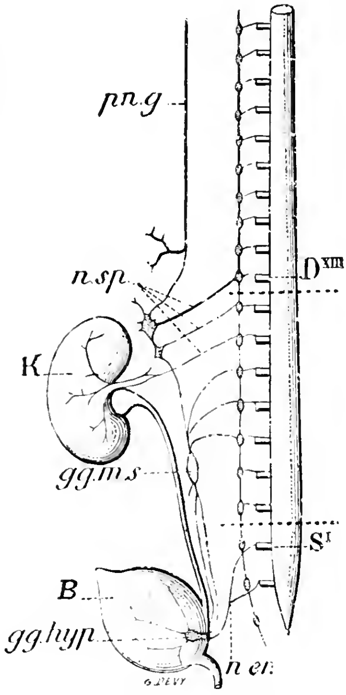


FIG. 144.—Innervation of the kidney and of the bladder.

K, kidney; B, bladder; Dxiii, thirteenth dorsal root (in the dog); S^1, first sacral; *pn.g*, pneumogastric; *n.sp*, splanchnic nerves (great and small); *gg.m.s*, superior mesenteric ganglion; *gg.hyp*, hypogastric ganglion or plexus; *n.er*, erector nerve.

C. TRANSMISSION AND CENTRALIZATION OF IMPULSES—THE MEDULLA OBLONGATA

The medulla oblongata is, as its name implies, a prolongation of the spinal cord in the encephalic cavity. The fundamental constituent elements of the spinal cord may here also be observed, with their primary arrangement still very obvious; but very important changes have also occurred, and new formations have been superadded.

Delimitation.—The spinal cord only derives its external stimuli from the organs of *touch*. The medulla oblongata, in addition to that of touch, enters into relation with other senses, and, if we were not bound down by morphological definitions, we should comprehend under this expression of "prolonged spinal cord" all formations of grey matter where the peripheral neurons of the *sensorial* paths come to a direct termination. In any case, we may conventionally associate with it those grey areas from which the sensori-motor nerves arise at the level of the pons and of the aqueduct of Sylvius, as being an obvious prolongation of the grey medullary axis.

Proper functions.—The medulla oblongata not only collects impulses provided by the organs of the senses, but, by means of new connexions

and formations, it elaborates and transforms these impulses whatever be their origin, in order to adapt them to aggregations of functions more complex than those of the spinal cord properly so called. From this point of view the medulla oblongata acquires a hierarchical superiority over the last-named, of the same nature as that possessed by the brain over it, as well as over the spinal cord.

Two orders of centres.—The medulla oblongata, as from the physiological point of view we must conceive it to be, and so as not to describe it exclusively from an anatomical aspect, but also from a functional one, will then comprehend two modalities of grey matter, namely: the first, which purely and simply continues what are called the *nuclei of origin* of the peripheral nerves, and the second, which is without any direct relationship with these origins themselves, but which inaugurates these *superposed systems* which are here progressively developed: at the base of the brain in its ganglia, behind it in the cerebellum, at its convexity in the cortex.

Motor and sensory nuclei.—The motor nuclei are genuine grey nuclei, in which are situated the origins of the efferent neurons, in every way resembling those of the anterior spinal roots, and which receive their proportional part of the cerebral neurons, which descend from the cortex to distribute its specific excitation to them. The sensory bulbar nuclei, if it be wished to assimilate them anatomically to the motor nuclei, are really constituted by the ganglia of origin of the trigeminal (or of Gasser), of the vagus (or jugular), of the glosso-pharyngeal (or of Andersh), etc., which continue the series of the spinal ganglia of the posterior roots. But the point of view of development is here the secondary one, and that of the transmission of impulses is, on the contrary, essential. But from this latter point of view the sensory nuclei of the medulla oblongata are grey masses receiving the terminations (emissive or transmissive poles) of the afferent neurons coming from the periphery, and which on their part send a proportional number of fibres of projection to the cortex by the fillet (*ruban de Reil*), which they help to enlarge. These sensory nuclei repeat the arrangements of those of the spinal cord. As regards the same root, and even as regards the same fibre of each root, they are multiple; for these roots and fibres bifurcate into ascending and descending branches, and one fibre of (for example) the trigeminal thus bifurcated will seek in the grey medullary substance (or even lower) localities analogous to the column of Clark, to the grey peri-ependymal substance, and to the nuclei of Goll and of Burdach. We may even remark concerning these two latter nuclei, that, though included in the conventional limits of the medulla oblongata, they really belong to the spinal cord, as they are in direct relationship with its special roots.

Grey reticulated bulbo-pontine substance.—The superadded grey masses belong especially to the reticulated bulbar and pontine substance. Though often diffuse, they are occasionally concentrated into distinct nuclei like the nuclei of Roller, in which it is supposed are represented *the respiratory centre, the vaso-motor centre*, and the nucleus of the tegmentum (calotte). These grey masses, which are no longer the direct origins of motor nerves, nor receptive of the direct extremities of the sensory nerves, are nevertheless united to these nerves, since they govern them; and, further, they are not without relationship with the brain, which under certain circumstances has power over them.

Their functions are especially *reflex*. The associations between sensory and motor nerves effected in the spinal cord are mere rough sketches when compared with those of the medulla oblongata; the former necessarily remain local and

give rise to movements which are also limited, and often without much functional significance, at least in the superior animals. On the contrary, the sensory impulses which attain the medulla oblongata find there much more favourable conditions of reflective association, this being displayed by more powerful movements, some, indeed, revealing a great tendency to generalization.

Analytical study; Division.—The analytical study of the medulla oblongata from a functional point of view comprehends then the functions of its white tracts, which are more especially conductors of the second order, participating in the conscious voluntary functions (those of the first order, which are none other than the cranial nerves, have been previously studied); also the already specialized reflex functions, which find here the conditions necessary to their existence. On account of the proximity of the centres of origin of the bulbar nerves to the reflex centres belonging to the medulla oblongata itself, it is not always easy to decide whether a given reflex act results from a simple association on the spot between the nuclei of origin of the bulbar nerves, or whether it is caused by the participation of a superadded centre. But this difficulty is not peculiar to the medulla oblongata; the spinal cord also presents it, as its grey matter encloses elements of association mixed with its exogenous elements. It is these which, assuming in the medulla oblongata an importance they did not possess in the spinal cord, bestow upon it its special functional significance.

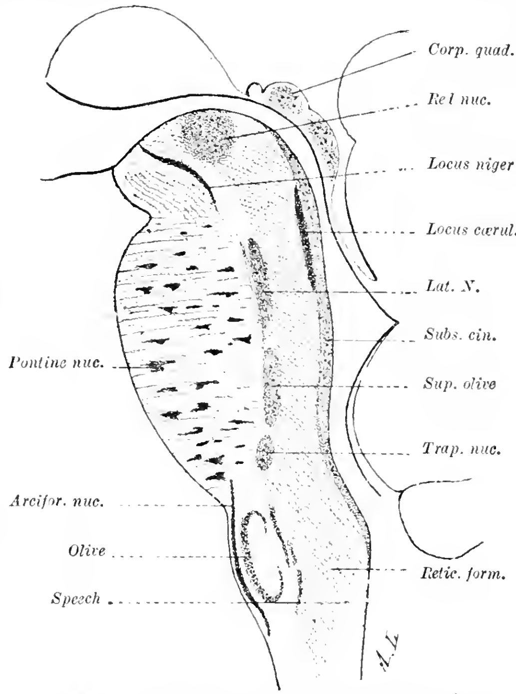


FIG. 145.—So-called ganglionic grey matter of the cerebral trunk (after Charpy).
Grey masses superadded to the sensori-motor nuclei.

1. Sensibility and Motricity in the Medulla Oblongata

A. MOTOR PATHS; ANTERIOR PYRAMID.—At the inferior portion of the medulla oblongata the anterior columns (descending) partially cross from one side to the other, on the median line. This decussation, which is here made *tract by tract*, renders visible to the naked eye an arrangement of the same nature, very general in the whole extent of the encephalo-medullary nervous axis, where it is made, *fibre by fibre*, and hence is rendered visible only by histological methods. It must be remembered that the decussation of the pyramids is only a fraction of their total crossing (even including only the descending fibres);

that it is incomplete at the level of the medulla oblongata (direct tract; crossed tract); and that it does not by itself explain the connexion which, in motor paralyses, unites the hemisphere of one side to the muscles of the opposite side.

Stimulation.—Longet, Laborde, and more recently Wertheimer and Lepage, have directly stimulated the anterior bulbar pyramids and have seen this stimulus produce movements in the muscles of the opposite side. If these tracts are cut, stimulation of the inferior end has the same result. There can then be no doubt that *the anterior bulbar pyramid possesses a motor function* which at first sight appears to be conferred upon it by its continuity with the motor tracts of the corona radiata and those of the spinal cord, as also by its connexions (by the aid of these tracts) with the motor area of the cortex on one hand, and with the anterior horns of the spinal cord on the other. The counterproof of this may be effected by cutting all the bulbar tracts, except the pyramids; it is found that in this case stimulation of the motor cerebral area still produces movements in the limbs (Brown-Séquard).

Section.—The bulbar pyramid is a motor path descending from the cortex to the spinal cord, but it is not the only one, as is proved by the following experiments, which in their turn serve as the counterpart of the preceding ones. If the two anterior bulbar pyramids be cut, the animal will not have lost all power of movement of its limbs. At first the movements may be disturbed and more or less hindered, but after a certain time, they become normal, and to such an extent that it becomes difficult to notice any alteration depending on this suppression (Langley and Grünbaum, Herzen and Loewenthal). In an animal which has undergone this section, stimulation of the motor area still produces localized movements in the limbs, though less marked (Unverricht).

Thus, whether by section around it, we oblige the descending impulse to pass through the pyramid, or whether, by section of the latter itself, we prevent it from thus passing there, the impulse finds a passage in the bulbar paths. We are not authorized to say that these paths are rigorously equivalent, and it is improbable that they are so. If they appear to us as being such, it is no doubt because we do not know how to distinguish the differences characterizing the functions subsisting in each case. We may in any event admit that after the suppression of the one there is a re-education of the nervous system and a tendency to substitute one for the other; a substitution, a re-education which are indicated by the time which must elapse before the more or less complete re-establishment of the function.

Decussation.—The bulbar pyramid is only partially crossed (bundle by bundle) with that of the opposite side, at the conventional limit of the spinal cord and of the medulla oblongata. The crossed part pene-

trates into the lateral column of the spinal cord on the opposite side ; the direct path remains on the same side (direct pyramidal tract, or tract of Türck), and penetrates into the anterior column of the spinal cord on the same side. It is very generally maintained that the direct tract decussates, in its turn, fibre by fibre, in the spinal cord, by its commissures ; but neither anatomy nor physiology gives a decisive proof either for or against this decussation. The most probable explanation seems to be that it is not total, but that the impulse descending from one of the halves of the brain remains partially in the corresponding half of the spinal cord and goes partially to the muscles of the opposite side. In this respect a univocal and absolute formula would be incorrect ; for both from a physiological and clinical point of view it has been found that certain movements are bilateral, and others unilateral, according to the necessities of the function ; finally, other movements may be also crossed according to the circumstances with which they are associated, bilateral in certain cases, unilateral in others.

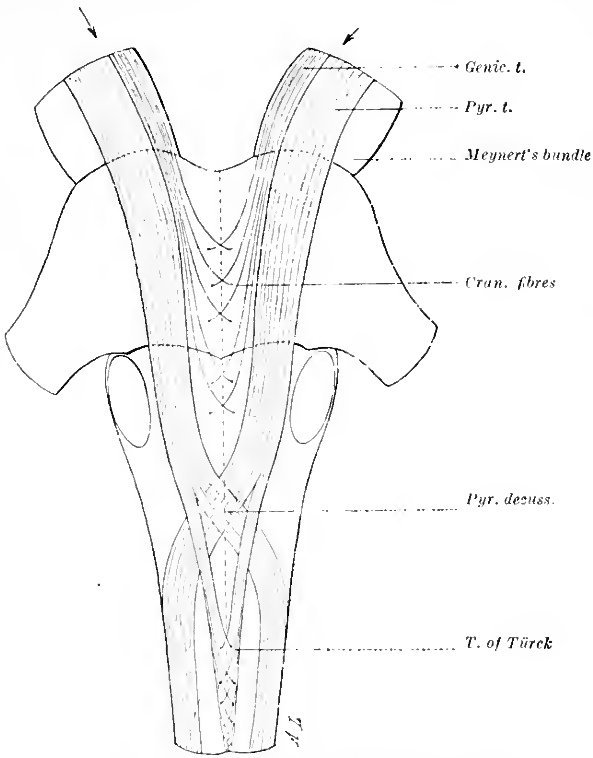


Fig. 146.—The pyramidal tract (after Charpy).
The geniculated or cranial tract, and the tract of Türck are decussated fibre by fibre.

The question of unilaterality or bilaterality has been raised as regards the crossed as well as the direct pyramidal tract. Pitres and Dignat, Dejerine and Thomas, have frequently noticed that, in addition to the direct tract which follows the anterior column, there is another direct tract following the lateral column on the same side. Further, decussation of the pyramids may, as these authors have noticed, present a great number of variations, even to the point of being sometimes entirely wanting. In animals, the direct pyramidal tract as it exists in man (tract of Türck, going to the anterior spinal column of the same

side) is lacking; it is replaced by a direct tract going to the lateral column of the same side, consequently similar to that pointed out in man by Pitres and Dignat, and which, in all probability, functionally replaces it.

A longitudinal section effected in the anterior furrow of the medulla oblongata, consequently cutting the decussation, produces a certain degree of paresis, that is to say, enfeeblement of the four extremities, but without entirely paralysing them: this affects the side opposite to the hemisection. A hemisection of the bulb above the decussation will also produce a weakening of the four extremities, but without paralysing them entirely; the weakness affects the side opposite to the hemisection. These two results support the view that there is a mixture in each half of the bulb of fibres destined for the two halves of the body and generally in unequal proportions.

So far, no distinct functional attribution for the crossed and the direct tract has been discovered. This last tract does not extend beyond the inferior limit of the dorsal region, which indeed it scarcely reaches. None of them takes part in attaching it to the innervation of the muscles of the trunk. As, in animals, the two tracts are confounded in the lateral column, isolated stimulation of these parts is impossible.

Alternate hemiplegia.—Gübler was the first to draw attention to a form of hemiplegia which attacks the face on one side (that corresponding to the lesion) and the limbs on the opposite side, and which is caused by a lesion limited to half of the medulla oblongata or of the pons above the decussation. A lesion thus situated attacks simultaneously the peripheral neurons of the facial of the corresponding side (consequently not decussated) and the deep neurons of the muscles of the limbs, which decussate a little lower down.

B. Sensory paths; fillet (ruban de Reil).—At the back and a little above the decussation of the anterior pyramids (therefore in the thickness of the bulb itself) another decussation will be found, which is effected by the sensory paths, and which closely repeats the preceding one. The crossed sensory tract (consequently ascending) commences in the nuclei of Goll and of Burdach and ascends to the cortex, with or without interruption (and this is the point under discussion) in the optic thalamus. This crossed sensory tract is duplicated laterally by a direct tract arising from the grey medullary substance, and these two tracts united form the fillet (*ruban de Reil*). This tract is again slightly enlarged in the medulla oblongata, by the addition of fresh sensory paths (also crossed) proceeding from the nuclei of the trigeminal, the glosso-pharyngeal and the vagus, and also by that of sensorial paths proceeding from the glosso-pharyngeal (taste) and from the acoustic (audition).

Clinical experience has collected a certain number of observations which tend to prove that hemianæsthesia (of the opposite side) is the consequence of the interruption of the fillet (or ruban de Reil); but insensibility has also been observed to result from bulbar lesions other than those of the fillet. There is then for the sensory, as also for the motor paths, a certain amount of uncertainty as to the functional part

played by these different conductors, or, in other words, concerning the conditions proper to each tract in the exercise of sensory functions.

Alternate hemianæsthesia.—Alternate hemianæsthesia has been described of which the mechanism is functionally similar to that of the hemiplegias of this nature. A lesion localized in one of the halves of the organ would affect simul-

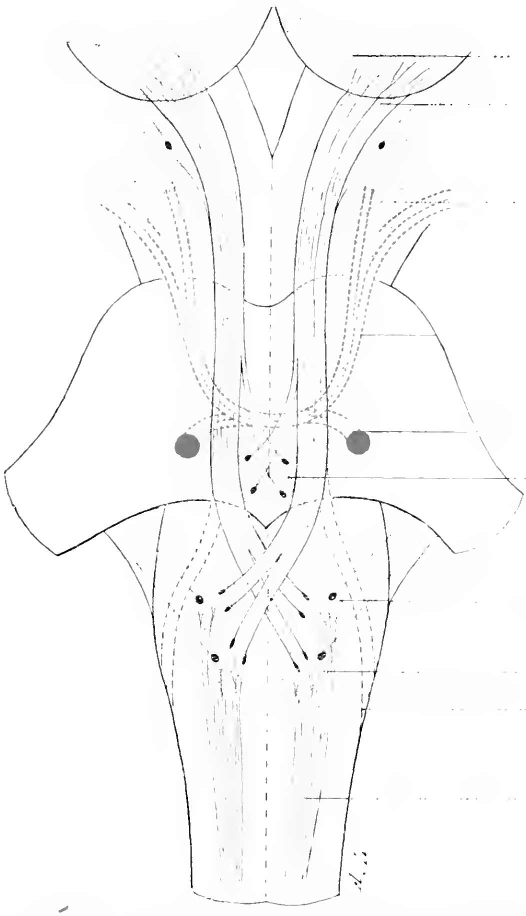


FIG. 147.—The fillet (*ruban de Reil*) or sensory tract (after Charpy).

The central acoustic path (acoustic tract, lateral fillet, ruban de Reil) is indicated in red. Diagram.

taneously the peripheral neurons (not decussated) of the trigeminal and the deep neurons (decussated), corresponding to the sensory nerves of the limbs.

Physiological experiment reproduces this form of hemianæsthesia by hemisection of the bulb. It is possible to verify, as the result of this operation, a diminution of sensation in the half of the body of the opposite side, and a hyperæsthesia of the corresponding side, as Brown-Séquard has pointed out in hemisection of the spinal cord; anæsthesia of the surface of the same side, as Magendie has observed; and finally those trophic disturbances of the ball of the eye which

usually accompany section of the trigeminal, and also follow section of its roots as Duval and Laborde have verified.

Expression of the emotions.—The movements of the face, due to the contraction of its cutaneous muscles which are supplied by the facial, are called *expressive*, because they markedly take part in the expression of genuine or feigned *emotions* and *passions*.

2. Local Reflexes

The fillet (*ruban de Reil*) and the anterior pyramid are paths appertaining, the first to *conscious* sensibility, and the second to *voluntary* movement. They are both connecting paths, extended in two different directions, between the cerebral cortex and the grey matter of the spinal cord and medulla oblongata. Their suppression prevents, or at least in a certain degree disturbs, the manifestations of consciousness and of the will. The medulla oblongata contains other associations which can dispense with the cortex, and, isolated from it, suffice for the regulation of certain functions of a reflex order. These connexions are effected in its grey matter; they are of two orders. The first simply unite between themselves the motor origins and the sensory terminations of the bulbar nerves for the performance of simple reflexes: they may be called *immediate centres*, or those of the first degree. The second are associations superposed to the grey nuclei of subjacent origin (medullary and bulbar) and which are *mediate centres*, or those of the second degree. This co-existence of centres belonging to two different orders in regions in the immediate vicinity of the grey matter is due to the fact of the medulla oblongata containing, as has already been mentioned, both the continuation of the column of origin of the peripheral nerves and fresh superadded formations, which are no longer original centres like those of the spinal cord. These formations have already, in some degree, acquired the power of autonomy, so highly developed in the brain; only they exercise it no longer in the manner of an action varied and contingent, as does the brain; but, on the contrary, in a regular and periodic fashion, whence the name of automatic centres sometimes applied to them.

As regards the internal functions ensuring nutrition (respiration, circulation, excretion, etc.) the impulse is automatically renewed in organs placed in *closed chains*. In the external functions which maintain our relations with other living beings, the renewal of impulse becomes in a manner fortuitous. Here the cycles present the appearance of a *chain open* to the exterior. The medulla oblongata is a rough sketch of these systems of relation by the help of which the animal *expresses* what it has *felt* by a defensive motor or even conventional manifestation. A cry is a manifestation of this nature; there is a reflex cry of purely bulbar origin.

1. **Reflex cry.**—In an animal which has undergone supra-bulbar section of the encephalon, stimulation of the sensory nerves produces a short unmodulated cry, which has been compared by Vulpian to that elicited by pressure on dolls made as playthings for children. This cry is obviously of reflex origin, and has some analogy to the cry which is known as *meningitic*.

The cry, like phonation, is an adaptation of the respiratory apparatus (essentially of internal function) to an external function, by an alteration in the connexions uniting its elements between themselves and with the neighbouring elements; the system of respiratory nerves becomes that of nerves of phonation, or, according to the usual expression, the respiratory centre becomes that of phonation.

The cry is the rough sketch of phonation, of language such as it exists in us. For the production of articulated speech a nervous stimulus is required, into which the medulla oblongata enters as a component part, and one which is superposed to a definite region of the cerebral cortex. In this extension of the cycle the cerebral cortex does not purely and simply take the place of the bulbar centre, but utilizes the relatively simple organization of the latter for the performance of a more complex act.

2. **Winking of the eyelids.**—The medulla oblongata controls sensibility and movement of the face, the first by means of the trigeminal, the second by that of the facial. These nerves are connected in the medulla oblongata for the performance of defensive reflexes, of which the winking of the eyelids, to cause removal of tears, furnishes an example. This movement is a correlated one, the two eyelids being lowered and raised together at the same moment. This correlation is due to a partial decussation, or to elements of association which cause the stimulation (reflex) reaching the nucleus of one side, to be transmitted to that of the opposite side. If an antero-posterior section between the nuclei of the two nerves is made exactly in the median line, this correlation ceases; winking of the eyelids can then be performed independently either on the right or the left side (Vulpian).

From this experiment may be deduced the physiological proof that the decussation of fibres belonging to the facial, if it exists, is not complete, for, if it were so, the median section would bring about paralysis of both sides.

3. **Conjugated deviation of the eyes.**—Certain functions require a succession of muscular efforts for the attainment of the end in view (the peristaltic movement of the digestive tube, movement of the limbs in walking). Others demand fixity and parallelism of these efforts; such is that of binocular vision when the conditions as regards the

formation of retinal images and of the superposition of two images are assumed to be normal. The association of the two eyeballs, which strictly solidarizes their movements, is attributed to anatomical arrangements, themselves consequently of a fixed order. These arrangements, which allow of some variation according to the authors who have described them, are all based on general principles, namely: that a motor stimulus, reaching the abductor muscle of the eye on one side must of necessity affect at the same time and to the same degree of intensity an adductor muscle of the eye of the opposite side, and reciprocally.

Duval and Laborde maintain that the nucleus of the abducens, or sixth nerve, supplying the right external rectus, also contains the origins of the branch to the internal rectus of the opposite eye; in reality, this aberrant branch arises from the nucleus of the sixth nerve, follows the posterior longitudinal bundle, decussates with its homologue below the corpus quadrigeminum, and, contained in the trunk of the abducens (sixth nerve) of the opposite side, is detached to go to the right internal rectus muscle. The impulse leaving the brain would only have to be directed to the nucleus of the sixth nerve to cause the eyes to be deviated in any given direction. Others consider (Spitzka) that the branch of the internal rectus also decussates in the median line, but its own nucleus does not form a part of the nucleus of the sixth nerve, but of that of the oculo-motor nerve. According to this hypothesis, an impulse coming from the brain is simultaneously directed to the nucleus of the sixth nerve and to the fraction of the nucleus of the oculo-motor nerve containing the origin of the branch of the opposite internal rectus. The connexion causing the co-operation would not be effected by the nucleus receiving the impulse, but by the elements bringing it there. Theoretically the solutions of this problem do not greatly differ.

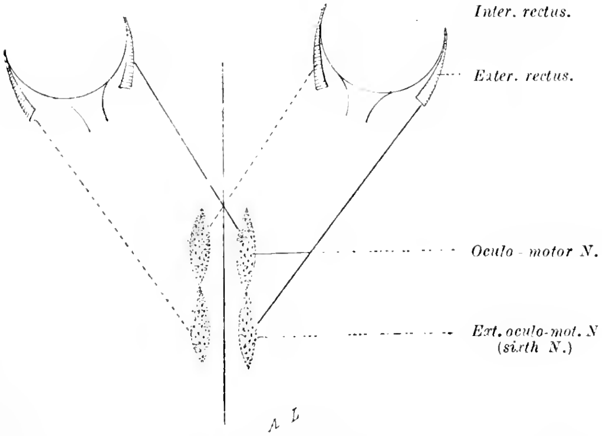


FIG. 148.—Co-operation of the nuclei of origin of the sixth and third nerves.

The partial nucleus of the internal branch of the third nerve regarded as a dependence of the nucleus of the sixth nerve.

Convergence for adaptation to distances.—In reality the visual axes of each eye are not parallel, but converge on the object looked at, and are the more convergent in proportion as the object is nearer. The fixity of the angle of convergence is then not constant, and the magnitude of this angle changes with the distance. To increase this value it is necessary for the contraction of the internal rectus muscles to

slightly surpass that of the external rectus muscles ; and for this to come about the impulse must be distributed in slightly predominating quantity to that portion of the nucleus of the oculo-motor nerve which contains the origins of the fibres proceeding to the internal recti.

Partial nuclei.—Anatomically the nucleus of the oculo-motor nerve is subdivided into a series of partial nuclei, corresponding to its different branches, and therefore to each of the recti or obliqui muscles, in addition to the nuclei answering to the internal musculature of the eye. These last are situated nearer to the median line, and rather in the superior portion of the origins of the third nerve ; the others are outside and prolonged lower down. These facts have been verified by effecting the isolated ablation of the peripheral muscles and observing, by means of the method of Nissl, the chromatolytic alterations of the cells of origin.

Functional dissociation.—By localized stimulation of each of these partial nuclei, experimental determinations have been made which nearly correspond with those effected by anatomical means (Hensen and Völkers).

4. **Sympathetic origins.**—The nuclei of the recti and obliqui muscles are the continuation of the direct motor origins of the nerves of the life of relation, which terminate at this level.

The nuclei of the internal muscles of the eye (ciliary muscle of accommodation and sphincter muscle of the iris) are not the equivalent of the preceding.

The fibres arising from them do not go directly to the deep muscles of the eye, but are fibres of projection of the second order, which stop in the ganglia and the ciliary plexus. These fibres contain the spinal origins of the great sympathetic, to which they belong, and of which they also mark the highest point of emergence in the grey axis.

Apparatus of association ; posterior longitudinal bundle.—The grey bulbar matter acts as an associating agent with regard to a large number of motor nerves, spinal as well as bulbar, for the performance of a certain number of definite functions. The impulses conveyed to it, not only by the nerves of touch, but also by those of the superior senses, are here reflected to the motor nuclei of the eyes and of the trunk by a special apparatus of association, *the posterior longitudinal bundle* or *posterior longitudinal tract.* This structure is situated on each side of the median furrow, below the floor of the fourth ventricle and of the aqueduct of Sylvius ; it is the continuation, and the equivalent, but in a more differentiated form, of the antero-lateral column of the spinal cord. It is formed by neurons of association, which receive the impulse coming from the sensory neurons by one of their poles, and by the other transmit it to the motor neurons. It brings into relation the sensory bulbar nuclei and the corpora quadrigemina, more especially with the motor nerves of the eyes and of the trunk.

5. **Deglutition.**—At the entrance of the digestive paths we are confronted by an act which forms the transition between those of the external and those of the internal functions : this is deglutition, which commences with an act of conscious sensibility and voluntary move-

ment and is completed by reflex movements. Once again it is the medulla oblongata which is the locality for the organization of the system subserving deglutition, the conducting fibres, both sensory and motor, of this system being met with in a certain number of bulbar nerves, namely, the trigeminal (mylo-hyoid muscle), the facial, the hypoglossal, and the vago-spinal, which perform the function of motor nerves connected with the sensory elements contained in the palatine nerves (of the superior maxillary), the superior laryngeal nerves, and, lastly, the glosso-pharyngeal, which are less essential than the preceding. The point of departure is the irritation of the bolus of food occurring at the level of the isthmus, on the extremities of the palatine nerves. The laryngeal nerves intervene to defend the entrance of the respiratory paths.

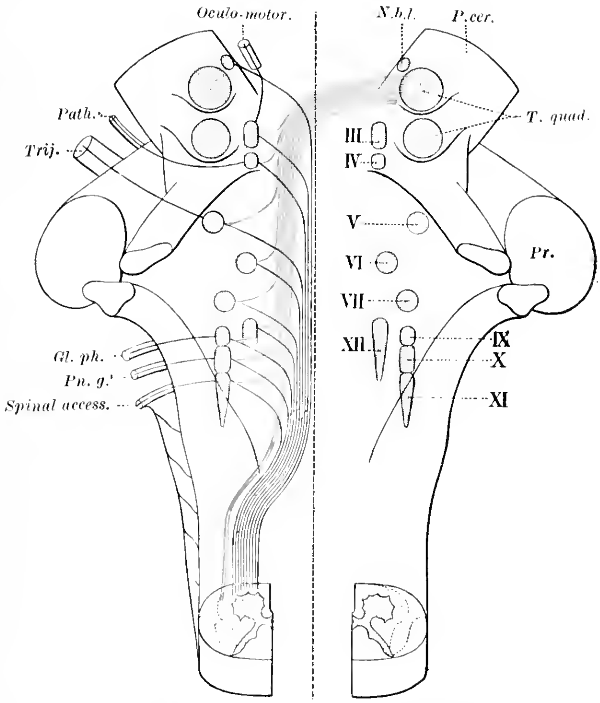


Fig. 149.—Posterior longitudinal bundle.

N.b.l, special nucleus of the longitudinal bundle; *P.cer*, crus cerebi; *T.quadr*, corpora quadrigemina; P. pons.—III to XII, nuclei of origin of the cranial nerves, bearing the number corresponding to the usual classification.

The grey matter of the spinal cord is united to that of the bulbar nuclei, and the two together to the corpora quadrigemina, by neurons of association or intercentral neurons whose union forms the longitudinal bundle. These neurons have different directions, some ascending (in black), others descending (in red).

The centre of association of these different nerves is situated between two planes, of which the superior passes through the acoustic tubercules, and the inferior through the apex of the calamus; according to Markwald, a little above and outside of the grey wing, above the respiratory centre. Sections made above or below the limits just pointed out permit of the persistence of swallowing (life being maintained by artificial respiration). The succession of peristaltic movements, which continue from the pharynx to the œsophagus, is assured by a regular transmission of impulses passing through the successive nuclei of the

motor nerves which control the pharyngeal and œsophageal constrictors.

6. **Mastication, suction.**—Like the preceding, these acts are of reflex nature. They are performed after the removal of the brain in young animals when an appropriate sensory stimulus is applied (Gads, Brown-Séquard), viz.: touching of the anterior portion of the buccal mucous membrane, irritation of the tactile extremities of the trigeminal. The nerves of the special senses do not intervene. The fifth pair is associated with both a sensory and several motor nerves, namely: motor branch of the trigeminal (mylo-hyoid muscles, anterior belly of the digastric, and external pterygoid), facial (muscle of the lips and stylo-hyoid), hypoglossal (muscles of the tongue and sub-hyoidean muscles). The reflex on the corresponding side is suppressed by a section separating the sensory nuclei and motor nuclei of the trigeminal.

3. General reflexes

The sensori-motor functions, which are carried out by the connexions of the grey bulbo-pontine substance, appertain in both consciousness and unconsciousness, and the boundary dividing these is often indefinite, or but little marked. We may form a conception of this by the help of some significant examples of both kinds, namely: as regards the first, phenomena of sensation and of locomotion; as concerns the second, regulating action on the functions of nutrition, respiration, circulation, secretion, etc.

1. **Common sensorium.**—The *substantia reticularis grisea* which, at the level of the pons, surmounts and continues the reticulated substance which is properly bulbar, brings about the sensori-motor associations already noticed by Lorry, and which, according to Longet and Vulpian, give it the value of *a common sensorium*.

In a mammal from which the cerebral hemispheres, the optic thalami, all the encephalon with the exception of the cerebellum, the corpora quadrigemina, the pons and the bulb have been removed, stimulation of a sensory nerve provokes motor reactions of an obviously painful character. This stimulation arouses prolonged plaintive cries, entirely different from the short, in a sense mechanical, cry of the animal deprived of the pons while the bulb is left intact. These painful cries are accompanied with laboured respiration and attempts at flight; all these being reactions which, at first sight, do not differ from those of an animal retaining the brain. Sensation must then exist, as it is manifested by those characteristic signs by which we are accustomed to recognize it. The difference in this case, is, that it leaves no persisting trace behind it, *is not accompanied by memory, but disappears*

with the motor reactions which have served for its external manifestation. From the fact of this non-preservation of sensation, the phenomenon is entirely reflex, but is at the same time painful ; that is to say, conscious. The phenomenon is a transitional one, leading to the effects resulting from the intervention of the brain, in which, on the contrary, the character of immediate reflexion disappears more or less completely in proportion as the phenomenon of conservation of sensation or of memory becomes more marked. In this simple reflex, where the traces of sensation are unrecognizable, the phenomenon is *excito-motor ;* in the reflex, accompanied with sensation, but without memory, the phenomenon is *sensitivo-motor* or *sensori-motor ;* in the case where reflex succession has in its turn become unrecognizable, by the interposition of cerebral acts of intelligence, the phenomenon is *ideo-motor* (Carpenter).

2. **Locomotive functions.**—A function which also implies, in the motor order, associations of a complicated nature, is locomotion in vertebrata, and especially in mammals ; and, combined with it, is standing in the upright attitude. As Longet has shown, the pons plays a part, not certainly exclusive, but essential, in this function.

Part played by the pons.—After the ablation of the cerebral hemispheres and the optic thalami in a rabbit, if the pons be left intact the animal will be seen to assume the ordinary attitude of repose ; if excited, it performs some regular steps, and then again becomes motionless. It will even sometimes make some steps without apparent provocation, no doubt incited by some internal stimulus. *If the pons is destroyed, all locomotion becomes impossible,* and the animal can no longer stand upright on its paws. Experiments of the same nature on animals of different classes, birds, fish, batrachia, give the same results. Locomotive power is more independent in these animals than in mammals. In fish, ablation of the brain, with preservation of the parts representing the pons, allows of the subsistence of a sort of spontaneity, no doubt apparent, and which is due to the persistence of the stimuli to which the animal left in its own medium is exposed. A frog with the brain removed remains motionless ; placed in water it swims (by reflex stimulation from the medium) until it reaches the edge, when it again becomes motionless. A bird after ablation of the brain, if placed on the ground, also remains motionless ; thrown in the air, it flies, to sustain itself until it once more falls to the ground. In both cases the mechanism is the same.

A voluntary impulse transmitted from the brain to the pons finds in this organ a ready formed nervous mechanism which it puts into

action, and by which complicated movements are brought about, without its taking part in their detail. It acts itself as a stimulus conveyed from the exterior by the sensory nerves.

Pre-established associations.—The functional associations effected in the pons for the performance of locomotion are the result of embryological development, and are not acquired by education. At least this may be asserted with regard to certain species both of mammals and birds. The young of the rabbit do not walk until they are several weeks old; it is the same with dogs, and several birds (pigeon, sparrow, etc.). On the contrary, the guinea-pig can walk as soon as it is born; and so can the chicken and the duckling. Every one is acquainted with the fact that ducklings hatched by the hen will take to the water directly they leave the egg, and swim without any need of apprenticeship or imitative education. It may also be allowed that, in man himself, walking and the upright position are facts of development rather than of education.

A. Respiration.—Experiments have long shown that the survival of animals is compatible with mutilations, with very extensive curtailments of the nervous system, when these are effected on its superior portion (brain, cerebellum, basal ganglion), or on the inferior portion (spinal cord as far as the neighbourhood of the middle of the cervical region); while very limited lesions brought to bear on the intermediate region may bring about death in a sudden manner, and without any return of the functions (Galen, Lory). This is because, as Legallois has pointed out, the mutilation at this point attacks nervous organs governing *respiration;* and, although this function in itself may not be more important than others (alimentation for example), the movements maintaining it can suffer *no delay*, because *the reserves of oxygen* are, in the organism, extremely *small* in quantity in proportion to those of other substances. If pulmonary ventilation, oxygenation of the blood and of the tissues is arrested, the general sequence of functions is interrupted; life cannot be maintained.

1. **Vital knot.**—Legallois observed that the lesion may be limited to a small space near the origin of the pneumogastric nerves. Flourens endeavoured to define still more clearly the locality of this area, which he calls *central motor of respiration*, or *vital knot* (nœud vital). After some alterations he located it in the depth of the bulb at the tip of the **V** of grey substance enclosed in the posterior angle of the fourth ventricle, and he extended it to right and left of the median line for about two or three millimetres from the latter, for this centre is double; respiration and life only cease when both sides are destroyed. The operation was performed by plunging a punch of the dimensions indicated into the bulbar matter.

Dissociation of the respiratory movements.—If the lesion is made immediately behind the tip of the **V**, the respiratory movements of the trunk are abolished,

those of the face, however, subsisting some time longer; if made immediately in front of the **V**, the converse happens; the movements of the trunk persist, while those of the face are abolished.

Situation and depth.—Longet, who has repeated these experiments, maintains that the mutilation producing these effects must bear upon the lateral tract of the bulb.

In endeavouring to perform the experiment of Flourens, a considerable number of observers have been induced to displace or extend the respiratory centre whose limits were fixed by him. From the contradictions which have arisen between them on this subject, Wertheimer draws the conclusion that it is not possible to limit this centre in a more definite manner than Legallois has done. It is a locality of grey substance enclosed in the inferior triangle of the floor of the fourth ventricle and comprehending its deep layers.

According to an arrangement which is found in all systems of the same nature, the bulbar centre of Legallois is superposed to the medullary centres from which the motor nerves of respiration directly emanate. It associates and co-ordinates them, making use of their aptitudes. Reduced by the separation of the spinal cord and of the medulla oblongata to the employment of their own unaided functions, these latter can still for a time maintain rhythmic movements capable of oxygenating the blood.

These movements of spinal origin are not observable in the conditions habitual to the destruction of the bulb, or to the experiment of Flourens, because the shock of operation prevents their production, and respiration, allowing of no delay, death at once supervenes. This difficulty is removed by maintaining artificial respiration until the effects of the shock are dissipated (Wertheimer), or by re-awakening the medullary excitability by strychnine (Langendorff), or by rhythmically exciting the sensory nerves of the thorax, which permits of respiration being maintained by exclusively spinal reflexes (Chauveau).

Respiratory hemiplegia.—According to Schiff, hemisection of the spinal cord below the bulb produces respiratory hemiplegia, by rendering a portion of the diaphragm and the corresponding muscles immobile. But this hemiplegia is not constant, and, when the stimuli are exaggerated, the paralysed side participates in the ventilation of the lung. If, for example, the phrenic nerve of the side opposite to the hemisection be cut, it is the side of the hemisection alone which contracts. Commissures existing between the nuclei of the phrenic nerve would ensure this transmission of impulses.

It is possible by a longitudinal section to separate the two halves of the medulla oblongata: respiration persists and remains synchronous; or, on the other hand, the two halves of the cervical spinal cord may be separated, and the result is the same. Connexions exist in both cases sufficient to solidarize the two halves partially separated.

2. **Influence of the composition of the blood.**—Like all centres of the same order, the respiratory centres operate in a reflex manner under the influence of the impulses which they receive by their sensory nerves; but they are further affected by the quality of the blood passing through them. *The lowering of tension of oxygen in the blood, the augmentation of that of carbonic acid, increases their excitability.* The movements of respiration are augmented. The conditions of vitiation of the internal medium are thus the same as those which increase the removal of its gases, and permit the ventilation to be regulated according to the composition of the blood.

Defensive reflexes.—The regular movement of respiration is converted, under certain influences, into a defensive movement of expulsion by exaggeration of the expiratory current of air, as in coughing and sneezing; these reflex acts are brought about by special sensory stimuli limited to certain regions, acting on mucous membranes either in their normal condition or after having undergone a certain amount of inflammation.

Cough.—Cough arises from stimulation of the extremities of the laryngeal nerves (principally the superior laryngeal), and preferably in certain localities. An area very efficacious for the production of cough (in the normal condition of animals) is the interarytenoid space of the glottis, towards the posterior extremity of the vocal cords (Vulpian). To a slighter degree, the areas innervated by the recurrent provoke coughing, even after section of the superior laryngeal nerves (Longet), and bring about the expulsive cough which protects the respiratory tracts during swallowing. Other areas of this description exist in the pharynx and in the soft palate, in the nasal fossæ, in the auditory meatus, etc.

Direct stimulation of the floor of the fourth ventricle produces coughing.

Sneezing.—The starting point of the stimulus is not the organ of olfaction, but the sensory elements of the olfactory mucous membrane furnished by the trigeminal (ethmoid filament of the ophthalmic branch). Neither is it the stimulation of the retina, when sneezing results from the impression produced by a vivid light, but it lies in the extremities of the ciliary nerves (Wertheimer and de Surmont).

Vomiting.—In the reflex act of vomiting, contraction of the diaphragm (modified respiratory movement) is associated with movements of the mouth and contractions of the stomach. The principal association of the sensori-motor nerves of these different organs occurs in the medulla oblongata. A dog subjected to the influence of tartar emetic, after sub-bulbar section of the spinal cord, merely performs movements of the mouth and neck without any rejection of food (Gianuzzi). Nevertheless, the possibility of acting in a reflex manner on the diaphragm, after section of the spinal cord, is demonstrated by stimulation of the central end of the splanchnic nerve (Luchsinger).

B. Circulation.—Like those of respiration, the stimulating and regulating systems of the movements of circulation are numerous, and formed of layers, to which localities of the grey matter, having for function the realizing of associations of their constituent parts, correspond. Here again we find inferior centres and a superior centre governing the latter. The inferior centres are, above all, the ganglia of the great sympathetic, whence directly proceed the vaso-motor and cardio-motor nerves, which form, between these ganglia and the cardiac and vascular muscles, fibres of projection of the first order. These ganglia are united to the spinal cord by communicating white branches, these, therefore, being fibres of projection of the second order. The points of penetration, or rather of exit, of these fibres of the second order (consequently intercentral) along the course of the spinal cord is very precisely known. We are much less well informed with regard to the relations entered into by them with the grey medullary matter. After leaving the apparent origins which we recognize as being theirs, do they ascend directly as far as the grey medullary matter, or are they

reinforced in the grey medullary nuclei which correspond to them ? Or, once again, do they present a mixture of these two arrangements ? These different opinions have all had partisans.

1. **General bulbar vaso-motor centre.**—It is especially to physiology that we look for a solution of this problem. The centres thus sought for are indicated functionally by the tonic action which they exert on the vascular pressure. By making progressive sections, or by destroying given areas along the grey axis, and noticing each time the state of the pressure, we shall see, by its changes or its persistence, if these centres exist or are wanting, and in what their function consists.

Spinal and ganglionic centres.—Sub-bulbar section of the spinal cord at first produces a considerable fall of pressure. This very evident fact has been brought forward as proof of the existence of a general and single centre, situated in the medulla oblongata, in the neighbourhood of the calamus (Schiff). But if, by artificial respiration, the life of the animal be prolonged, it will be seen after a certain time that the vascular tonicity is re-established and the pressure raised. It may be increased by asphyxial stimulation, or by the action of strychnine ; the remaining tonic power is then shared by the spinal cord and the ganglia of the great sympathetic. By an experiment of the same nature consisting in removal of the largest part of the spinal cord, Goltz and Ewald have also shown that, after a fresh fall, the vascular tonus may be re-established by the only subsisting action, that of the great sympathetic. It is better then to refrain from judging directly from the immediate effect, which is not definitive, but to realize that, after a period of shock, the system, in spite of its equilibrium being thus destroyed, retains in itself the means of re-establishing to a certain degree the disturbed function, and employs for this purpose the resources of its associations still left intact. From what has just been said, it is proved that these associations exist in the ganglia, in the spinal cord, and in the medulla oblongata, these latter possessing the very highest importance for the regulation of the vaso-motor function.

2. **Vaso-motor reflexes.**—Another property of the centres is that of reflecting impulses conveyed to them by the path of the sensory nerves. Stimulation of an important sensory nerve, such as the trunk of the sciatic, produces, by reflex action, a marked elevation of pressure. If by successive operations different portions of the brain and the encephalon are removed, these reflex actions still remain possible as long as the medulla oblongata is intact (Dittmar). They cease directly the bulb is separated from the spinal cord (Owsjanikow). These experiments seem in a very distinct manner to define at the same time both the situation and the limits (in height) of the vaso-motor centre. They

also indicate the bulb as containing this centre, which is at the same time single and independent. They certainly give it a preponderating importance, but they ought to be verified by other and decisive proofs.

Here again it is necessary to distinguish between immediate and consecutive results. Once the shock of the operation over, it may be possible that the sensory stimulus (even in the case of sub-bulbar section) may exert its reflex effect of elevation of pressure. It must be then that the stimulated sensory nerves reach in the spinal cord itself centres of reflexion resembling the bulbar centre, which are less powerful, that is to say, less qualified, for generalizing the stimulus to the whole vaso-motor system, but able to perform this function to a certain degree. The bulbar centre may, for its part, under certain conditions, obey the impulses descending from the cerebral cortex.

Cardio-inhibitory centres.—Thus there is in the medulla oblongata a centre for the association of impulses which harmonizes other centres of association placed in dependence on it. These are gradated in the grey bulbo-medullary axis in such a manner that those placed highest are situated almost in the immediate neighbourhood of the vaso-motor centre. Amongst these are the nuclei of origin of the cardio-moderator nerves contained, according to certain authors, in those of the pneumogastric; others, it is true, locate them a little lower, in those of the spinal accessory (Waller); of this number also are the nuclei of origin of other vaso-motor nerves (principally dilators), going to the tongue, to the sub-maxillary gland, etc. The medulla oblongata, the thoracic and the sacral spinal cord, are, as has already been said, the three principal localities (at least apparently so) for the origin of nerves which either by the sympathetic chain (thoracic region), or outside it (bulbar and sacral region), proceed to the heart and the vessels. A characteristic feature of the medulla oblongata is that of being at the same time a *continuation of the spinal cord* by the nuclei of origin prolonging the grey axis, and also a *superadded formation*, by the supplementary grey masses which have no longer any connexion with the periphery except by the preceding nuclei, to which they are united by links, contributing to form the white tracts of the spinal cord and of the bulb.

C. Movements of the pupil.—The movements of the pupil, which are very easy to observe, have also served for determining the connexions of the great sympathetic with the spinal cord and the medulla oblongata.

1. **Dilator reflex of the iris.**—The apparent origin of the dilator nerves of the pupil is in the cervico-thoracic region of the spinal cord. Budge localizes a *cilio-spinal* centre in this region. Chauveau has observed that, if the spinal cord be cut in the cervical region (between

this centre and the bulb), stimulation of a posterior thoracic root will still cause the pupil to dilate by reflex action on the spinal cord. The bulbar centre is not indispensable for this reflexion. Some authors have noticed the possibility of this effect being induced after the separation of the bulb (Salkowsky). It must be remembered that the medullary power of reflexion is impaired by the shock succeeding the section, and reappears only after a certain period of repose. And it must also be noticed that the dilators of the iris arise not only from the thoracic spinal cord by the cervical great sympathetic, but also from the special origins of the trigeminal itself, by fibres representing the cranial or bulbar portion of the origins of the great sympathetic, and that after the separation of the spinal cord and the bulb, these latter being put out of court, the dilatory action of the stimulation is by just so much diminished. The irido-dilator reflex in these experiments has a sensory stimulus for starting point (posterior root or some kind of sensory cutaneous nerve).

2. **Irido-constrictor or photo-regulative reflex.**—Another reflex exists which is antagonistic to the preceding one, and has for its starting point a sensorial stimulation of the optic nerve, revealing itself by the contraction of the pupil at the approach of a strong light. This reflex, pointed out for the first time by Herbert Mayo, has the retina and the optic nerves for its centripetal paths, the anterior corpora quadrigemina for locality of reflexion, and for paths of return to the constrictor muscles of the iris, fibres which, arising in one of the partial nuclei of the oculo-motor nerve, follow this nerve, pass through the ophthalmic ganglion, to terminate by ciliary nerves in the ciliary plexus and by it in the iris. This reflex system, instead of having its paths divided between the spinal cord and the medulla oblongata, has them, on the contrary, concentrated in this latter organ and in the nerves which either start from it or terminate in it. In any case, if there are medullary paths, there are no means of demonstrating their existence.

Whether one or the other of these two reflexes is in question, there are certainly, in addition to local centres of emergence of the motor nerves and of termination of the sensory nerves, one or more centres of association. For the photo-regulatory reflex these centres are near each other (corpora quadrigemina, nuclei of the oculo-motor nerve, longitudinal bundle): for the irido-dilator reflex they are separated by a great distance (medulla oblongata, thoracic spinal cord, ground bundle); thus their experimental dissociation becomes easy, and when effected by section of the cervical spinal cord, it shows that the reflex associations persist in the inferior centre between sensory and motor nerves brought into relation by its grey matter.

D. Secretions.—The preeeding scheme is applicable to the vasomotor system, and also to that of the secretory nerves. Whether the

cutaneous covering or the intestine with its large appendant glands be in question, it is almost superposable to it. The same distribution of nerves to the periphery; the same origins in the chain and in the spinal cord and the medulla oblongata; the same subordination of inferior systems to a bulbar centre of association, and the same conditions bringing into relief the predominating part played by this centre and the existence of the inferior systems.

In the restricted space allotted to the respiratory centre, and to the general vaso-motor centre, experiment demonstrates the existence of other localities of association, which act in an analogous manner on the phenomena of glandular activity. The influence of the medulla oblongata extends to the renal secretion, the secretions of the digestive tract, and the cutaneous secretion; it also governs what are called *internal secretions*, of the same nature as that of the formation of glucose at the expense of glycogen of the liver. This is proved by the following facts.

Diabetic puncture.—*Glycosuria.*—Cl. Bernard has shown that by puncturing the floor of the fourth ventricle at a given point, situated on the median line and in the space which separates the origin of the two pneumogastrics, the appearance of sugar in the urine is provoked; the glycosuria commences from the first hour following the operation and disappears after four or five hours: from this we may conclude that the puncture acts as a stimulus.

Polyuria.—If the puncture is effected a little higher, in the space comprised between the origins of the acoustic and pneumogastric nerves, *polyuria* and glycosuria will appear simultaneously. These two phenomena are further most frequently associated.

Albuminuria.—If the puncture be carried out still higher up, between or above the origin of the acoustic nerves, polyuria alone may appear, with or without *albuminuria.*

Salivation.—Cl. Bernard has also noticed that salivation may be provoked by puncturing the fourth ventricle. The occurrence of glycosuria suggests the existence of a connexion between the bulb and the liver, this latter being the glyco-secretory organ, and the more so because, after the puncture, an elevation of the proportion of glucose in the arterial blood is observed, and this effect (hyperglycæmia and glycosuria) no longer results when the branches of the great sympathetic running to the liver have been previously cut.

Polyuria points to a connexion with the kidney, and hypersalivation to one with the salivary glands.

Reflex secretions.—These different glandular activities may be provoked in a reflex manner by stimulation of certain sensory nerves. Hyperglycæmia has been observed after stimulation of the central end of the vagus (Cl. Bernard), glycosuria and hyperglycæmia after that of the depressor nerve (Filehene, Laffont). These reflex effects are no longer produced when the region in the bulb corresponding to the point where the puncture is made has been destroyed.

Sudation.—Stimulation of the sensory nerves usually produces a

reflex action of the sweat glands. Without seeking to define narrowly the region where this reflexion occurs, the question has been raised (just as it has been for the vaso-motor nerves) as to whether the spinal cord or the medulla oblongata, or both together, are concerned in it, and if so, in what measure. While the medulla oblongata retains its connexions with the spinal cord, reflex sudation is easily effected. After sub-bulbar section, according to some authors, this reflexion ceases (Nawrocki); according to others, it persists in a restricted manner (Luchsinger, Robillard). This latter opinion is the true one; only it is necessary that stimulation should not be applied for a certain time (perhaps twenty minutes, or half an hour) after section of the spinal cord, to allow time for the shock of the operation to pass off: life is maintained by pulmonary insufflation.

Connexions between parallel systems.—As a whole, the systems governing the circulatory and secretory functions closely resemble each other. Their nerves pass into the chain and the ganglia of the great sympathetic: for the same organs they are contained in the same trunks and leave the spinal cord by the same roots. We have just seen that these systems possess a common locality of systematization in the grey substance of the medulla oblongata, without prejudice to those which they present in the sympathetic ganglia and in the spinal cord. This vicinity of their elements and this penetration of their centres indicate functions which are not only parallel, but in a certain degree dependent the one on the other, or which are at any rate regulated the one by the other. These functional associations imply connexions, in the different localities of the grey matter, between the two systems. The grey masses which we call vaso-motor, secretory, or other centres, should therefore be considered not as organs with definite boundaries, but, once again, as a complex assemblage of connexions which can be made or severed according to the requirements of the function.

BIBLIOGRAPHY.

Spinal Cord.

Various functions.—Aducco, Fonct. vaso-motr., *Arch. ital. de biol.*, 1891.—Arétée, Morb. acut. et diuturn., lib. I.—Aladoff, *Bull. Acad. St-Pétersbourg*, 1869.—Cl. Bernard, Leçon sur la physiol. du syst. nerveux.—Bickel, *Arch. f. Anat. und Phys.*, 1900, pp. 481 et 485.—Birge, *Arch. f. Anat. und Phys.*, 1882, p. 481.—Brown-Séquard, Rech. et exp. sur la physiol. de la moelle épinière, thèse inaugurale, Paris, 1846; *Gaz. hebd.*, 1855; *Journ. de la phys. de l'homme et des animaux*, 1858–1863; *Arch. de phys.*, 1868 et suiv.—Calmeil, *Journ. des progrès*, 1828.—Celse, De locis affectis, lib. IV, cap. VII; De admin. an. lib. VIII, cap. VI, VIII, IX.—Chauveau, *Union méd.*, 1857; *Journ. de. phys.*, 1861.—Edw. Flattau, Innerv. muscl. bras et mains de l'homme, *Arch. f. Anat. und Phys.*, 1899.—Flourens, Rech. exp. sur les prop. et fonct. du syst. nerv., 2 édit., 1840.—Gad, *Arch. f. Anat. und Phys.*, 1883, p. 438, et 1884, p. 304.—Goltz, Moelle lombaire, *Arch. de Pflüger*, 1872 et 1874.—Joteyko, *C. R. Acad. sc.*, 1900, t. CXXX, p. 667.—Legallois, Œuvres complètes, Paris, 1830.—Longet, *Arch. gén. de méd.*, 1841.—Magendie, *Journ. de la phys.*, 1823; Leçons sur les fonct. et les maladies du syst. nerv., 1839, t. II, p. 153.—Mendelssohn, *Arch. f. Anat. und Phys.*, 1885, p. 288.—Regas-Nicolaïdès, Trajet des vaso-moteurs, *Arch. f. Anat. und Phys.*, 1882.—Ollivier, Traité des maladies de la moelle épinière.—Is. Ott, *Journ. of Phys.*, 1879–1880, vol. II, p. 42.—Paladino, *Arch. ital. de biol.*, 1895, t. XXII, p. 39.—Paton, *North. Americ. Med. Chir. Review*, 1855.—Porter, Voies resp., *Arch. f. Anat. und Phys.*, 1894.—Stilling Unters. üb. d. Fonct. d. Rückenmark, Leipzig, 1841.—Schiff, *Pflüger's Arch.*, 1880.—Setchenow, Reflex hemmend. mecan., *Arch. de Pflüger*, 1875.—Van Kempen, *Journ.*

de la phys., 1859.—VAN DEEN, Traités et découvertes sur la physiol. de la moelle épin., Leyde, 1841; *Froriep's Neue Notizen*, 1843.—VULPIAN, Art. "Moelle," *Dict. de Dechambre* (bibliographie).—WALLER, *Biol.*, 1855.—WERTHEIMER, *C. R. Acad. sc.*, 1886, t. CII, p. 520.

Posterior columns.—BECHTEREW, *Arch. f. Anat. und Phys.*, 1890, p. 489.—BROWN-SÉQUARD, *Journ. de la physiol. de l'homme et des animaux*, 1863.—ENGELKEN, *Arch. de Du Bois-Reymond*, 1867, p. 198.—FODERA, *Journ. de phys. expér.*, 1823, t. III, p. 191.—GIANNUZZI, *Centralbl.*, 1873, p. 824.—JACOB et BICKEL, *Arch. f. Anat. und Phys.*, 1900. —PFLÜGER, Die sensorisch. Fonct. d. Rückenmarks.—PIERRET, *Arch. de phys.*, 1872, p. 364.—ROLANDO, *Journ. complém. du Dict. des sc. méd.*, 1828, t. XXX, pp. 159 et 204.—SCHIFF, *C. R. Acad. sc.*, 1854 et 1862; *Lehrb. d. Phys.*; *Gaz. hebd.*, 1859 et 1872.—SCHÖPS, *Arch. de Meckel*, 1827; *Journ. complém. du Dict. des sc. méd.*, 1828, t. XXX, p. 114.—TROISIER, *Arch. de phys.*, 1873, t. V, p. 709.

Anterior and lateral columns.—DITTMAR, *Sächs. Ges. d. Wiss.*, 1870.—HUIZINGA, *Pflüger's Arch.*, 1870, t. III, p. 81.—MENDELSSOHN, *Arch. f. Anat. und Phys.*, 1883, p. 281.—MISCHER, *Arbeit. phys. Anstalt. zu Leipzig*, 1870.—NAWROCKI, *Arbeit. phys. Anstalt. zu Leipzig*, 1870.

Hemisection of the spinal cord.—BOTTAZZI, *Arch. ital. de biol.*, 1895, t. XXIV, p. 466. —HOMEN, Lésions par hémisect., *C. R. Acad. sc.*, 1883, t. XCVI, p. 1681.—OPPENHEIM, Zur Br. Seq. Lähmung, *Arch. f. Anat. und Phys.*, 1899, Suppl. p. 1.

Trophic disturbances.—ANGELUCCI, Œil, *Arch. ital. de biol.*, 1894, t. XX, p. 67. BENTIVEGNA, Vague et symp. pneum. expér., *Arch. ital. de biol.*, 1895, t. XXIV, p. 243. —BROWN-SÉQUARD, *Biol.*, 1850, et *Journ. de la phys.*, 1863.—G. FANTINO, Myocarde, *Arch. ital. de biol.*, 1888, t. X, p. 237.—FLORESCO, *Arch. des sc. médicales*, 1899 et 1900.—MORAT et DOYON, *C. R. Acad. sc.*, 1897, t. CXXV, p. 124.—MORPURGO, Régén. cell. paralys. vaso-mot., *Arch. ital. de biol.*, 1890, t. XIII, p. 342.—SALVIOLI, *Arch. ital. de biol.*, 1895, t. XXII, p. 259.

Different degenerations and alterations.—DEJERINE, Altér. des nerfs cutanés de escarres, affect. médull., *Arch. de phys.*, 1882, t. IX, p. 499.—GRUNBAUM, *Journ. of Phys.*, 1894, vol. XVI, p. 368.—GURRIERI, Empoisonnem. phosphoré, *Arch. ital. de biol.*, 1896, t. XXVI, p. 370.—LAMY, Embolies expérim., *Arch. de phys.*, 1895, p. 77.—SHERRINGTON, Second and tertiar degen., *Journ. of Phys.*, 1885, p. 177.—SPRONCK, Anémie passagère, *Arch. de phys.*, 1888.—TSCHIRIEW, Lèpre, *Arch. de phys.*, 1879, p. 614. —VASSALE et DONAGGIO, Altér. après extirp. glandes para-thyroïd., *Arch. ital. de biol.*, 1897, t. XXVII, p. 124.

Spinal cord in those who have undergone amputation.—HAYEM et GILBERT, *Arch. de phys.*, 1884.—PELLIZI, *Arch. ital. de biol.*, 1893, t. XVIII, p. 26.—VULPIAN, *C. R. Acad. sc.*, 1872, t. LXXIV, p. 462.

Great Sympathetic.

Constitution and relations.—BIRGE, Nombre des fibres et des cellules, *Arch. f. Anat. und Phys.*, 1882.—W.-H. GASKELL, *Journ. of Phys.*, 1886, p. 1.—LANGLEY, *Journ. of Phys.*, 1891, p. 375; Larger medull. fibres, *Ibid.*, 1892, p. 786.—MAGNIEN, Rapp. avec les. n. craniens, *C. R. Acad. sc.*, 1887, t. CIV, p. 77.—ROCHAS, Gangl. cerv. sup., *C. R. Acad. sc.*, 1887, t. CIV, p. 865.

Degeneration; regeneration: chromatolysis.—EVE, Activité et repos, *Journ. of Phys.*, 1896, p. 334; Action de la tempér., *Ibid.*, 1900, 1, p. 119.—LANGLEY, Régénér., *Journ. of Phys.*, 1895, t. XVIII, p. 280; Dégénér., *Ibid.*, 1900, p. 468.—LUBIMOFF, Atroph. muscul. progress. spinale, *Arch. de phys.*, 1874, p. 889.

Ganglia; reflex and inhibitory action.—DASTRE et MORAT, Pouvoir tonique et inhib., *C. R. Acad. sc.*, 1883, t. XCVI, p. 446.—FR.-FRANCK, *Arch. de phys.*, 1894, p. 717.—LANGLEY, Axon-reflex, *Journ. of Phys.*, 1900.—PHISALIX, Mouvements des chromatophores des céphalopodes, *Arch. de phys.*, 1892 et 1894.—P. SCHULTZ, *Arch. f. Anat. und Phys.*, 1898, p. 124.—WERTHEIMER, *Arch. de phys.*, 1890, p. 519.—WERTHEIMER et LEPAGE, *C. R. Acad. sc.*, 1899, t. CXXIX, p. 737.—WHITE, *Journ. of Phys.*, 1887, p. 66, et 1889, p. 341.

Innervation of the heart.—ENGELMANN, Méthode d'observ. *Arch. f. Anat. und Phys.*, 1900, p. 178 et p. 315.—HEYMANS, *Arch. f. Anat. und Phys.*, 1893.—LAHOUSSE, *Arch. f. Anat. und Phys.*, 1886.—NICOLAJEFF, *Arch. f. Anat. und Phys.*, 1893.

Periodic inexcitability; refractory phase; extra-systole; post-compensatory systole; conservation of the work of the heart, etc.—Voy. CIRCULATION (bibliographie du *Cœur*).—Myogenic and nevro-genic theories, Voy. *Dictionnaire de physiologie* de Richet, article "Cœur."

Accelerating innervation.—ALBERTONI et BUFALINI, *Ric. Gab. d. Fisiol. universita di Siena*, Milan, 1876.—BAXT, *Sächs. Ges. d. Wiss.*, 1875; *Arch. f. Anat. und Phys.*, 1878.—CL. BERNARD, Leçons syst. nerv., t. I, pp. 206 et 382, t. II, p. 449.—V. BEZOLD, *Acad. de Berlin*, 1862; *Journ. Br.-Séq.*, 1862; Sur l'innervation du cœur, Leipzig, 1863. —BUDGE, *C. R. Acad. sc.*, 1852.—E. et M. CYON, *Arch. f. Anat. und Phys.*, 1867;

C. R. Acad. sc., 1867 ; *Journal de l'anatomie de Robin*, 1868.—FRANÇOIS-FRANCK, *Biol.*, 1879 : *C. R. Acad. sc.*, 1879 ; Lab. Marey, 1878–79 ; *Biol.*, 1884.—LEGALLOIS, Sur le principe de la vie, Paris, 1812 ; Œuvres, 1811.—LUDWIG et CYON, *Centralbl. f. med. Wissensch.*, 1866 ; *Arch. de Du Bois-Reymond*, 1867.—LUDWIG et THIRY, *Wien Sitzungber.*, 1864.—MOLESCHOTT, *Revue hebd. de méd. de Vienne*, 1861, 1862, et *Molesch. unters.*, 1862.—MOLESCHOTT et NAUWERCK, *Molesch. unters.*, 1861.—MOLESCHOTT et HUFSCHMIDT, *Ibid.*, 1862.—REYNIER, Thèse agr., Paris, 1860.—SCHIFF, *Arch. f. phys. Heilk.*, 1849 ; *Lehrb. d. Phys.*, 1858 ; *Med. Centralbl.*, 1873.—SCHMIEDEBERG, *Arbeit. a. d. phys. Lab.*, Leipzig, 1871.—TRAUBE, *Berl. klin. Wochensch.*, 1866.—VOLKMANN, *Müller's Arch.*, 1845.—WERTHEIMER, *Echo médic. du Nord*, 1898.—WILSON PHILIPP, *Bibl. univ. de Genève*, t. I.

Moderating innervation.—Voy. CIRCULATION et NERFS CRANIENS, Pneumogastrique.

Vaso-motor and secretory innervations.—Voy. CIRCULATION et SECRETION.

Heart poisons.—CYON, *Revue générale des sciences pures et appliquées*, 1901.—FILEHNE, Nitrite d'amyle, *Arch. de Pflüger*, 1874, t. IX.—KLUG, *Arch. f. Anat. und Phys.*, 1879, 1880 (Digitale).—KRONECKER, Ether, *Arch. f. Anat. und Phys.*, 1881.—LANGENDORFF, Atropine, *Arch. f. Anat. und Phys.*, 1886.—SCHIFF, *Arch. de Pflüger*, 1871.—S. SCHMIDT, Chloroforme, *Arch. f. Anat. und Phys.*, 1897.—WEINZWEIG, Muscarine, *Arch. f. Anat. und Phys.*, 1882.

Cutaneous secretions.—ARLOING, *C. R. Acad. sc.* 1889, t. CIX, p. 785 ; *Arch. de phys.*, 1890 et 1891.—J.-N. LANGLEY, *Journ. of Phys.*, 1895, p. 296.—LUCHSINGER, *Arch. de Pflüger*, Série de mémoires, 1880 et suiv.—NAWROCKI.—VULPIAN, *C. R. Acad. sc.*, 1878.

Other cutaneous functions.—P. BERT, Nerfs colorateurs.—LANGLEY et SHERRINGTON. Pilo-moteurs, *Journ. of Phys.*, 1891, p. 278.—POUCHET, Color. chez les poissons, *C. R. Acad. sc.*, 1871, t. LXXIII, p. 943.

Uterus.—E. CYON, *Pflüger's Arch.*, 1873, t. VIII, p. 349.—FRANKENHAUSER, *Iena Zeitsch.*, 1865.—GOLTZ et FRENSBERG, *Pflüger's Arch.*, t. IX, p. 552.—HOFMANN et V. BASCH, Mouv. du col, *Wien. med. Jahrb.*, 1876 et 1877.—KÖRNER, *Phys. Inst. Breslau*, 3 cahier, 1863 ; *Centralbl. f. Med.*, 1864.—OSER et SCHLESINGER, *Centralbl. f. Med.*, 1879.—SCHLESINGER, *Wien. med. Jahrb.*, 1873, et 1874.—SPIEGELBERG, *Zeitsch. f. rat. Med.*, 3e série, t. II, 1857.—VULPIAN, Vaso-moteurs.

Vesiculæ seminales.—LOEB, *Dissert. Giessener Henle und Meissner Bericht. Phys.*, 1865.—RÉMY, *Biol.*, 1884.

Spleen.—CL. BERNARD, Lig. de l'organisme.—BOCHEFONTAINE, Th. doct., Paris, 1873 ; *Arch. de phys.*, 1874 ; *Gaz. méd.*, 1873.—MALASSEZ et PICARD, *Biol.*, 1878.—OEHL, *Gaz. méd. lomb.*, 1868.—PICARD, *C. R. Acad. sc.*, 1879.—ROY, *Journ. of Phys.*, 1882.—SCHIFF, Leçons sur la digestion.—TARCHANOFF, *Pflüger's Arch.*, 1873.—VULPIAN, *Biol.*, 1848 ; Cours de path. exp. et comparée, 1873.

Medulla Oblongata.

Paths of motor transmission : anterior pyramids : decussation.—BERGER, *Neurol. Centralbl.*, 1895.—BROWN-SÉQUARD, *Arch. de phys.*, 1889.—DEJERINE et THOMAS, *Biol.*, 1896.—HALLOPEAU, Des paralysies bulbaires, Thèse d'agrégation de Paris, 1875.—JACOBSOHN, *Neurol. Centralbl.*, 1895.—MAGENDIE, Leçons sur les maladies du syst. nerv.—PIERRE MARIE, Leçons sur les maladies de la moelle.—MURATOFF, *Arch. f. Anat.*, 1893.—NOTHNAGEL, Traité clinique du diagnost. des mal. cérébr., 1885.—PITRES, *Arch. de phys.*, 1884.—SHERRINGTON, *Journ. of Phys.*, 1885 et 1889 ; *British med. Journ.*, 1890.—UNVERRICHT, *Neurol. Centralbl.*, 1890.—WERTHEIMER et LEPAGE, *Arch. de phys.*, 1896.

Paths of sensory transmission.—AUERBACH, *Anat. Anzeiger*, 1889, et *Arch. f. Anat. und Phys.*, CXXI.—BERDEZ, *Revue méd. de la Suisse romande*, 1892.—BROWN-SÉQUARD, *Arch. de phys.*, 1889.—CONTY, *Gaz. hebdom.*, 1877 et 1878.—DEJERINE et SOTTAS, *Biol.*, 1895.—EDINGER, *Deutsch. med. Wochenschr.*, 1890.—FERRIER et TURNER, *Proc. of th. Societ.*, 1894.—FLECHSIG et HŒSEL, *Neurol. Centralbl.*, 1890.—LŒWENTHAL, *Revue méd. de la Suisse romande*, 1885.—P. MEYER, *Arch. f. Psych.*, t. XIII, 1882.—MOELI et MARINESCO, *Arch. f. Psych.*, 1892.—MONAKOW, *Neurol. Centralbl.*, 1884.—ODDI et ROSSI, *Arch. ital. de biol.*, 1891.—SINGER, *Sitzungsber. d. K. Acad. Wien*, 1881.—SINGER et MUNZER, *Denkschr. d. K. Acad. Wien*, 1890.

Alternate hemiplegia.—LABORDE, *Biol.*, 1877.—SENATOR, *Arch. f. Psych.*, 1881.—VULPIAN, Thèse de Paris, 1853, et *C. R. Acad. sc.*, 1885.

Vital knot.—BROWN-SÉQUARD, *Journ. de la phys.*, 1858.—FLOURENS, *C. R. Acad. sc.*, 1851 et 1858 ; *C. R. Acad. sc.*, 1847 ; *Soc. philom.*, 1849.—GALIEN, De anat. administr., Leipzig, 1821, lib. VIII, cap. IX, pp. 698 et 697, édit. de Kühn.—LONGET, *Arch. gén. de méd.* 1847.

Respiratory centre.—ADUCCO, *Arch. ital. de biol.*, 1899, t. XII, p. 99, et 1890, t. XIII, p. 89.—RICH. ARNHEIM, *Arch. f. Anat. und Phys.*, 1894, p. 1.—BROWN-SÉQUARD, *Arch. de phys.*, 1893, p. 131 ; *Biol.*, 1887.—CHRISTIANI, *Arch. f. Anat. und Phys.*, 1880, pp. 280 et 295, et 1886, p. 180.—FRÉDERICQ, Innerv. resp. chez le Poulpe, *C. R. Acad. sc.*, 1879, t. LXXXVIII, p. 346.—GAD, *Arch. f. Anat. und Phys.*, 1893, p. 175.—GAD et MARI-

NESCO, *Arch. de phys.*, 1893.—GIERKE, *Arch. v. Pflüger*, 1872, t. VII, p. 583.—GIRARD, Rech. sur l'app. resp., Genève et Bâle, 1891.—LABORDE, *Traité de phys.*—LANGENDORFF, Excitation . . ., *Arch. f. Anat. und Phys.*, 1881, p. 519; *Ibid.*, Insectes . . ., 1883, p. 80; *Ibid.*, 1887, p. 237; *Ibid.*, 1888, p. 283; *Ibid.*, 1893, p. 397.—LEWANDOWSKY, *Arch. f. Anat. und Phys.*, 1896, pp. 195 et 483.—LŒWY, *Arch. f. Anat. und Phys.*, 1887, p. 472.—NEWELL MARTIN et BOOKER, *Journ. of Phys.*, 1878–79, vol. I, p. 370.—MEYER, Innerv. resp. chez nouv.-né, *Arch. de phys.*, 1894, p. 472.—MISLAWSKY, *Centralbl. f. Wiss.*, 1885.—W.-T. PORTER, *Journ. of Phys.*, 1895, p. 455.—SCHIFF, *Arch. v. Pflüger*, 1870, t. IV, p. 225.—SPECK, Régulation . . ., *Arch. f. Anat. und phys.*, 1896, p. 465.

Phonation.—DUVAL et RAYMOND, *Arch. de phys.*, 1879.—FRAUSE, *Berlin. klin. Wochenschr.*, 1890.—RAUGÉ, *Arch. de phys.*, 1892, p. 730.—SEMON et HORSLEY, *Philos. Tran.* CLXXXI, p. 187.—VULPIAN, Leçons sur le syst. nerveux.

Mimicry.—BECHTEREW, *Arch. de Pflüger*, 1887.—BRISSAUD, Leçons sur les maladies du syst. nerveux, 1895.

Cough.—KOTHS, *Arch. de Pflüger*, 1874.—SCHIFF, Recueil de mémoires, II, p. 494.—VULPIAN, *Arch. de phys.*, 1882.

Sneezing.—LUCHSINGER, *Arch. de Pflüger*, 1882.—SANDMANN, *Arch. de Pflüger.*—WERTHEIMER et SURMONT, *Biol.*, 1888.

Vomiting.—HARNACH, *Arch. f. Path. und Pharm.*—HLASKO, Dissert. Dorpat; *Jahresb. f. Phys.*, 1887.—TUMAS, *Jahresb. f. Phys.*, 1887.

Co-ordination of the reflexes; convulsions.—BISWANGER, *Arch. f. Psych.* XIX.—HEUBEL, *Arch. de Pflüger*, IX.—LUCHSINGER, *Arch. de Pflüger*, 1878 et 1880.—LUCHSINGER et GUILLEBEAU, *Arch. de Pflüger*, XXVIII et XXXIV.—NOTHNAGEL, *Arch. f. Anat. und Phys.*, IV.—OWSJANIKOW, *Berichte d. Ges. d. Wiss. Leipzig*, 1874.—WERTHEIMER, *Journ. de l'anat.*, 1886.

Locomotion.—FANO, *Arch. ital. de biol.*, 1883.—SCHRADER, *Arch. de Pflüger*, 1887.—STEINER, *Jahresb. f. Phys.*, 1885.—TARCHANOFF, *Biol.*, 1895.

Blinking of the eyelids.—ECKHARD, *Centralbl. f. Phys.*, 1895.—EXNER, *Arch. de Pflüger*, VIII.—LABORDE, Traité de phys.—LANGENDORFF, *Arch. de Pflüger*, 1887.—MENDEL, *Berl. klin. Wochenschr.*, 1887.—NICKELL, *Arch. de Pflüger*, 1888. VULPIAN, *Sec. phys. coup. Syst. nerv.*

Mastication and suction.—BASCH, Succion, *Centralbl. f. Phys.*, 1891.—BROWN-SÉQUARD, *Biol.*, 1849.—GAD, *Arch. de Pflüger*, 1891.

Deglutition.—MELTZER, Irradiation . . ., *Arch. f. Anat. und Phys.*, 1883, p. 209.—STEINER, Schluck . . . und Athm . . . *Arch. f. Anat. und Phys.*, 1883, p. 57.—WALLER et PRÉVOST, Réflexe déglutit., *Arch. de phys.*, 1870, pp. 185 et 343.

Vaso-motor centre.—ADUCCO, *Arch. ital. de biol.*, XIV, p. 37.—DASTRE et MORAT, *Biol.*, *Arch. de phys.* et *C. R. Acad. sc.*, 1878 et suiv.—DEGANELLO, Act. tempér . . . *Arch. ital. de biol.*, 1900, t. XXXIII, p. 186. DITTMAR, *Bericht. d. Sachs. Gesellsch.*, 1871, p. 135, et 1873, p. 449.—OWSJANIKOW et TSCHIRIEW, *Bull. Acad. de Saint-Pétersb.* et *Arch. de phys.*, 1873, p. 90.—PIERRET, Relation entre le syst. vaso-mot. bulbe et moelle, *C. R. Acad. sc.*, 1882, t. XCXIV, p. 225.—SANDER et KRONECKER, Verbreitung der Gefässnerven Centren, *Arch. f. Anat. und Phys.*, 1882, p. 422.—SCHIFF, *Unters. z. Phys. d. Nervensyst.*, Francfort, 1855; Recueil de mémoires, II, 578.—STEFANI, Act. temperat., *Arch. ital. de biol.*, 1895, t. XXIV, p. 424.—VULPIAN, *C. R. Acad. sc.*, 1874, t. LXXVIII, p. 472.

Dilatation of the pupil.—CHAUVEAU, *Journ. de la phys.*, 1861.—FRANÇOIS FRANCK, *Trav. labor. de Marey.*—GRUENHAGEN, *Arch. de Pflüger*, XL.—GRUENHAGEN et COHN, *Jahresb. f. Phys.*, 1884.—HENSEN et VŒLKERS, *Arch. f. Ophtalm.*, 1878, XXIV.—KOWALESKY, *Arch. slav. de biol.*, I, p. 92.—LUCHSINGER, *Arch. de Pflüger*, XXII, 1880.—SALKOWSKY, *Zeitsch. f. rat. Med.*, 1867.—SCHIFF, *Phys. d. Nervensyst.*, 1858.

Sudoriparous secretion.—FREDERICQ, *Arch. de biol.*, 1882.—LUCHSINGER, *Arch. de Pflüger*, XVI.—NAWROCKI, *Centralbl. Wiss.*, 1879.

Biliary secretion.—HEIDENHAIN, *Herman's Handbuch.*—VULPIAN, *Biol.*, 1861.

Lachrymal Secretion.—SECK, *Journ. de la phys.*, 1885.

Digestive secretions.—HEIDENHAIN, Sécrét. pancréat., *Arch. de Pflüger*, 1875. MORAT, *Biol.*, 1894.—PAWLOW, *Arch. de Pflüger*, Suppl., 1893.—PAWLOW et SCHUMOVA SIMANOWSKAJA, *Centralbl. f. Phys.*, III.

Diabetic juncture.—CL. BERNARD, Leçons sur la physiol. expér., 1855.—CHAUVEAU et KAUFMANN, *Biol.*, 1893.—CYON et ALADOFF, *Bull. Acad. des sc. de Saint-Pétersb.* 1871.—HÉDON, Piqûre aprés extirp. du pancréas, *Arch. de phys.*, 1894, p. 269.—KAUFMANN, *C. R. Acad. sc.*, 1894, t. CXVIII, p. 894: *Arch. de phys.*, 1895.—KUHNE, *Gottinger Nachricht*, 1856.—SCHIFF, *Journ. de l'anat.*, 1866.—SPALITTA, Polyurie, *Sicilia medica*, 1889.—VULPIAN, Vaso-moteurs.

Functional associations of the bulbar centres.—BROWN-SÉQUARD *Journ. de la phys.*, 1858.—BURDON-SANDERSON, *Handbook of Phys.*, 1873, p. 315.—L. FREDERICQ, *C. R. Acad. sc.*, 1882.—HERING, *Sitz. Acad. Wien*, 1869.—KNOLL, *Sitz. Acad. Wien*, 1885.—MELTZER, *Arch. de Pflüger*, 1883.—STEINER, *Arch. de Pflüger*, 1883.—WERTHEIMER et MEYER, *Arch. de phys.*, 1889 et 1890.

CHAPTER IV

SUPERIOR SYSTEMATIZATIONS

Both morphologically and functionally, the nervous structures situated above the pons, the cerebellum and the brain, properly so called, form very important and highly differentiated systems. These systems are not in direct communication with the peripheral organs, some of which are receptive of impressions and others executive of functions. They receive impulses which have already been transformed and mutually associated in the spinal cord and the medulla oblongata ; they also act on motor associations belonging to these two organs, which are organized internally for the performance of definite acts or movements, whose realization they have the power of determining. They are still less the *efficient* cause of movement than are the inferior systems which they govern ; but are to a greater degree than these a *directing* factor in the transformations of energy which take place in the course of the performance of functions. By their hierarchical situation above the preceding, and by their internal organization, they bring about those syntheses which, in the order as much of sensation as of movement, produce unity of the functions, and by the mutual dependence and harmonious concordance of these latter, the unity of the *ego*.

A. ORIENTATION AND EQUILIBRATION ; THE CEREBELLUM

To the spinal cord and the medulla oblongata, which are in direct relation with the sensory and muscular organs, and which associate them in simple acts, sensitivo-motor cycles are superposed, representing elaborated systems.

These are more or less multiplied according to the degree of organization of the animal under consideration, and are variously differentiated according to the nature of its functions. They correspond to a division of the internal work of the nervous system.

They represent special modalities of the senso-motricity of which the reflex bulbo-medullary arc symbolizes the simplest form. United by the latter to the organs receptive of impulses and executive of movements, they adapt the bulbo-medullary system to determinate functions which differ according to each of them. In this way these superior systems employ the inferior ones to perform their functions ; for this purpose they have only to utilize the elementary associa-

tions prepared by the organization belonging to these simple systems, by incorporating them with the more extended and more specific associations which they bring into being. In this way these inferior systems execute acts whose complexity and variety go far beyond any of which they are capable when reduced to a state of isolation.

The cerebellum is a superior system of this nature. It has special relations both with sensation and motion. Its principal stimuli are derived from organs themselves of a special nature (semi-circular canals), as well as from touch and vision. It conveys the impulse in its turn to the muscles (principally to those of the life of relation), whose tonic activity it maintains, at the same time harmonizing their contractions, with the aim in view of maintaining the attitude of the body in the upright position and in walking.

Historical—The special situation and the external configuration of the cerebellum have given rise to a certain number of hypotheses concerning its functions which it is scarcely necessary to recall. Willis considered it to be the centre of organic functions. Rolando compared its layers to the couples of a galvanic battery and regarded it as a generator of motor force. Gall located here the inclination for physical love, and the instinct of the propagation of the species.

The experimental and analytical study of its functions begins with Flourens in 1824. The researches of this author have been made on a large number of species, principally on birds and especially on the pigeon, and also on mammals. His animals have survived, and so permitted him to observe the effects consecutive to ablation. His experiments, being very methodically carried out, have established very definite facts which, though elaborated by his successors, will continue to form the basis of all our knowledge with regard to the functions of the cerebellum.

Function of motor co-ordination.—He distinctly states that, after ablation of the cerebellum, sensation, intelligence and will are preserved: the animal has not lost the inclination for movement, but this, from being previously coherent and ordinate, has now become disordered, and no longer realizes the end which its will or instinct has in view. This disorder is the greater when the more co-ordinate movements are under consideration: in the bird which flies, flight would be of this number: in the case of birds which walk and swim, it would be walking and swimming. The movements of locomotion are lost, but those of conservation persist. If the cerebellum is removed in successive slices, layer by layer, this want of harmony goes on increasing; once the organ is removed, the animal is incapable of holding itself upright or of walking.

From these facts Flourens derives evidence of the existence of a function of co-ordination of movements (voluntary) whose seat is in the cerebellum. To attribute a function of co-ordination to this organ alone is no doubt to go beyond the demonstrated facts, and even the intention of the author; for he himself remarks that nutrition remains co-ordinated, and on the other hand we know that co-ordination of movements of locomotion may be destroyed by lesions of organs other than the cerebellum (locomotor ataxy of tabetic origin; lesion of the roots and the columns of the spinal cord).

In the adaptation of muscular movements to a definite function, like the maintenance of the upright position or walking, the part played by the cerebellum is not exclusive, but is nevertheless essential, and for want of a special term which

is still lacking to define this rôle, it has been found necessary for the sake of concentration to adopt one having a more general value.

The experiments of Bouillaud, Lussana, Wagner, Vulpian and many others have led these authors to the demonstration of facts which, as a whole, differ but little from those established by Flourens, and to conclusions resembling his. Lussana, in the interpretation he gives to these facts, considers the cerebellum as being the organ of the muscular sense. The localization attributed at the present day to the muscular sense is quite different; it is considered to be situated in the cortex of the central convolutions of the brain, in company with the sense of touch, of which it is a dependent form. So far as the muscular sense lies in the more or less distinct consciousness which we have of our muscles and of their state of contraction, this localization is not controvertible; but it must not be forgotten that, just as motricity has very various forms and expressions in the brain and the cerebellum, so also may sensation affect different modalities in the nervous organs which the centripetal impulse passes through before arriving at the cerebral cortex. The cerebellum receives from the muscles, and at the same time from the organs of touch, and of several other senses, impulses which are reflected by it under the form of movement, and so far it may be considered as an organ of sensibility, but of a sensibility which is not exclusively muscular.

The experiments of Majendie, Longet, and Schiff were directed more particularly to the cerebellar peduncles and to the movements of rotation resulting from their section.

Function of equilibrium.—Since Flourens, the most important work on the functions of the cerebellum is due to Luciani (1884–1891). The length of time his animals have survived the operation, the detailed study of symptoms and their evolution, the simultaneous study of structural anatomy unite in giving great interest to his work. Ferrier has also largely contributed to our knowledge of the functions of the cerebellum by the method of localized stimulations which he has applied to this organ. He substitutes electrical stimulation for the mechanical or chemical excitations employed by Weir-Mitchell and Nothnagel. Luciani carefully distinguishes between the symptoms due to *irritation*, those due to *deficiency*, and those of *compensation* or of *supplement*, which succeed each other, and sometimes co-exist in the intermediate phases. Following Leven, Ollivier, Luys, and Weir-Mitchell, he draws attention to the *diminution of muscular force* which is displayed after the period of irritation. The contractions are feebler *on the side corresponding to the lesion*: this is what he has named *asthenia*. The muscular tone is diminished, hence arise flexion of the limbs and frequent falls when in the erect position: *atony*. There are also tremors, oscillations and titubation, these being due to the fact of the nervous impulses not following each other with sufficient rapidity: this is *astasia*. Nevertheless, Laborde disputes these interpretations, and prefers to them the explanation of Flourens.

From these facts, Luciani concludes that the cerebellum has the power of augmenting the potential energy of the nervous system (sthenic, tonic and static action): this, however, is taking appearance for reality, no part of the nervous system being capable of furnishing potential energy to any nervous or non-nervous organ, but only having the power of causing it to dispense that which comes to it from food and is stored up in its reserves.

The weakening of the muscular tone following the destruction of the cerebellum is, nevertheless, a very real fact and has been proved by all experiments undertaken under the same conditions. The influence possessed by the cerebellum of maintaining the muscular tonus has, according to Ewald, its principal starting point in the impulses it receives from the vestibular nerve: the effects

of section of this nerve are similar to those caused by destruction of the cerebellum.

Trophic influence.—Removal of the cerebellum causes consecutive degenerations of various kinds, either in the bundles of fibres connecting it with the organs, or in the muscles or even the skin (Luciani). These disturbances of nutrition obey the general laws regulating the appearance and progress of degenerations consecutive to nervous lesions. The fibres when cut in their course undergo Wallerian degeneration; later, secondary atrophy may invade the nervous elements or the organs to which they are distributed.

COMPARATIVE ANATOMY.—The cerebellum is present in all vertebrata: its development is in relation to the complication of the conditions which ensure equilibrium in these animals. At least this is what stands out most markedly from a summary study of these conditions and of the comparative development of the organ in question (Thomas).

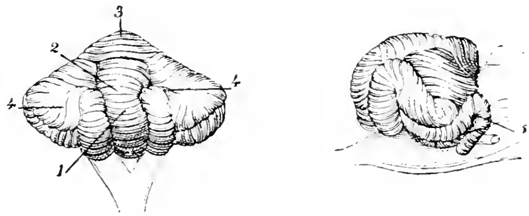


FIG. 150.—Cerebellum of the dog.
On the left, posterior and superior aspect; on the right, right external aspect.

1, pyramid of the middle lobe: 2, posterior extremity of the superior vermiform process; 3, its anterior extremity; 4, lateral lobe and its posterior-superior lobule; 5, flocculus (after Ferrier).

Reptiles.—The cerebellum can hardly be said to be present in reptiles, and is reduced to a transverse layer lying across the fourth ventricle (adder, toad, frog, lizard, tortoise, terrestrial salamander . . .), in the turtle it forms a globular mass larger than one of the optic lobes—in the crocodile it displays several folds, and two lateral appendices are observed (Leuret).

Fishes.—In fishes it is almost as reduced in size as in reptiles (Serres); it has the form of an elongated layer adhering in front, free at the back, attached to the sides of the spinal cord. In the dog-fish and the shark it possesses two lateral appendices.

FIG. 151.—Cerebellum of the monkey.
On the left, superior and posterior aspect; on the right, left lateral aspect.

3, superior vermiform process, behind which the middle lobe with its pyramid is seen: 4, lateral lobes with their semi-lunar lobule: 5, flocculus (after Ferrier).

In those animals which almost exclusively crawl on the ground or swim in the water, the conditions of equilibrium are simple. The same cannot be said as regards the two following classes.

Birds.—In birds the cerebellum assumes a considerable development: it is formed of a single median lobe presenting from ten to twenty parallel layers (Leuret). It is only in some kinds of birds that the median lobe is laterally enlarged (notably in the pigeon, the ostrich, the stork, etc.). According to Serres, this development is in agreement with the greater strength of the wings, and superior aptitude for flight. In birds, the fourth ventricle is prolonged into the cerebellum (ventricle of Malacarne). Thomas has observed that, contrary to the opinion of Serres, their cerebellum possess four nuclei, two larger lateral ones, probably corresponding to the ciliary bodies (corpora dentata), and two

smaller median, separated by the ventricle of Malacarne, which represent the nucleus of the roof. This author is convinced that the structure of the cerebellum is essentially the same in reptiles and birds as in mammals.

Mammals.— In mammals the lateral masses, hardly indicated in birds, assume a relatively considerable volume. The number of the layers is variable : 9 in the bat, 12 in the rat, 32 in the rabbit, 66 in the sheep, 75 in the ox, 175 in the horse. Still reduced in the rodents, the lateral lobes undergo progressive development in ruminating animals, in the solipedia, carnivora, and especially in the dolphin and the monkey. While the median lobe is inversely proportionate to the cerebral hemispheres, the lateral lobes are on the contrary directly proportionate to them. The functions of the first should then, according to Nothnagel, differ from those of the second, it being understood that no attempt is made to define the nature of either one or the other. With regard to this the opinion of Serres seems nearest the truth, and the cerebellar hemispheres should by preference take part in acts of a voluntary nature (Thomas).

1. Conditions of equilibrium

The conditions of equilibrium have been analyzed by authors who have studied this function experimentally, and especially by Thomas. The attitude of the human body and of that of animals in the upright position being assumed, equilibrium is effected, as we know, when *the axis of the centre of gravity falls within the polygon which represents the base of support.* The body is then subjected to two equal and contrary forces, one of which (weight) is represented by the axis indicated, the other (resisting force) by the supports (limbs of the animal) resting on the ground.

In the upright attitude.—These supports are articulated systems which, by contraction of certain of the muscles (extensors), the animal can cause to become rigid, and which he can also solidarize with the trunk by the contraction of other muscles. The trunk itself, with its superior prolongation (the head), is a system formed of mobile portions, which become rigid by contraction of the muscles inserted therein. This relative rigidity is thus obtained by the tonic action of a large number of muscles, whose efforts are antagonistic in numerous directions. The antagonism exists from one side to the other for muscles of the same name ; and from front to back for the posterior and anterior limbs of animals ; it also exists for the muscles of each segment of the skeleton considered in an isolated manner (extensors, flexors, adductors, abductors, rotators, in one or the other direction, etc.). *Preservation of equilibrium when standing still implies,* as is obvious, *a contraction, co-ordinated in extent and direction, of almost all the muscles of the body.*

In walking.—In walking the supports of the body undergo limitations and alterations as they succeed each other periodically, and at the same time they are carried, one in front of the other, in a definite

direction. In man these movements are produced alternately on one or the other foot ; in quadrupeds they are limited to three, then to two limbs, in a diagonal direction (ordinary walk, trot), or in an antero-posterior direction (amble). Equilibrium, threatened every moment, is re-established by compensating changes in the attitude of other parts of the body ; these changes having for their aim and object the continued retention of the axis of the centre of gravity in the more or less restricted area of the base of support (lateral oscillations of the trunk, rotation in an opposite direction of the pelvis and the shoulders ; antagonistic oscillations of the arm and of the leg of the same side, etc.).

Analogous compensations appear in all acts of a similar nature which require, as the essential condition of their performance, the preservation of equilibrium (running, jumping, etc.). All these acts expend a certain amount of muscular energy, which is employed in overcoming resistances and effecting movement in a definite direction ; but, further, another expenditure is demanded from the muscular tissue as a whole, in order to prevent falling ; this expenditure continues in the upright position, and only ceases during the total decubitus of the body in man or in animals when extended on a plane surface.

1. **Reciprocal relationship between the motor effect and the sensory stimulation.**—In order that the muscles of the body, by their aggregate contraction, may bring about these compensations, it is necessary that there should be developed through the nervous system *a cycle of stimulation in virtue of which the individual static contractions of all those muscles are regulated by the effect obtained*, ready to be reinforced in the direction of falling and to be moderated in the opposite direction. This, further, is the usual manner in which all the equilibria in the organism are effected, being, as they all are, of a mobile nature (circulation, respiration, calorification, composition of the blood, the humours, the organs, etc.). This is also a very general function of the nervous system, and the end aimed at by its organization is, as it were, the insurance of equilibrium in the animal economy. There is hardly any reflex system whose function does not participate in this.

The co-ordination of movements, of acts of whatever nature, is not then a specific function of a definite system ; but the equilibrium of our bodies in standing and in progression is a special case of co-ordination of movements, and, as such, possesses in the cerebellum its most differentiated representation.

It must, however, be understood that this differentiation does not imply isolation ; the cerebellum is a nervous organ superposed on inferior systems (spinal cord), in which motion is realized and co-ordinating action sketched out ; further, it is united to superior systems

which govern it and aid or supplement it, when its own action is wanting (optic thalamus, corpus striatum, cerebral cortex).

2. Sense of equilibrium.—We possess *a sense of equilibrium* which is a modality of what is still called *sense of orientation*, or *sense of space*. The word *sense* has in physiological language a very special signification, but it has also a general meaning, and this is the case here. A sense, properly so called, is defined, on the one hand, by the specific nature of the stimulus acting upon it (luminous or sonorous vibration, etc.); on the other, by the equally specific nature of the resulting sensation (visual or auditive, etc.).

We know of no stimulus or specific energy answering to the sense of space. It has been well said that the ideas of direction in space come to us by means of a special apparatus, the semi-circular canals, and it has been proved experimentally that the destruction of these canals brings about serious disturbances of equilibrium ; but experiment has also proved that, after lesion of these canals, this function may be re-established. Section of the two nerves of the eighth pair leads to disturbances of hearing (cochlear nerve), and also to those of equilibrium (vestibular nerve) ; after this mutilation, hearing is lost for ever ; equilibrium, on the contrary, becomes possible after some weeks have elapsed. Although the latter may receive its principal guidance from the semi-circular canals, it seems as if it also collects it elsewhere. Tactile, muscular, articular and visual sensations all contribute to the realization of equilibrium. Equilibration is not a specific sense, but a function which appeals to several senses ; there are as many ways of compromising it as there are senses taking part in it ; the deficiency of each of these may be more or less covered up by the supplementing and compensating action of the subsisting senses (Lugaro).

Not only do we find at the periphery neither a specific stimulus nor an exclusive organ adapted to the sense of space, but the impulses furnished by the semi-circular canals do not appear to reach the consciousness. Collected by a series of nuclei (nuclei of the roof, of Deiters and Bechterew, dorsal, descending), the impulses transmitted by the vestibular nerve are directed towards the cerebellum, the motor nuclei of the bulb (oculo-motors), and the superior portion of the spinal cord ; but no distinctly traced path for them as concerns the cerebral cortex is known. The fibres, doubtless but few in number, representing this path do not proceed to the auditory area, but rather to that of touch.

These impulses fall into a reflex system which regulates the position of the eyes, of the head, and of the trunk, and thus governs more or less directly the function of orientation and equilibrium, by an unconscious adaptation of the contractions of the muscles to this function.

Such of these impulses as reach the cerebellum act by means of this organ in quite as unconscious a manner on the muscular tonus, so as constantly to compensate for displacements (in standing or progression) by which the equilibrium might be jeopardized.

3. Automatic action.—Every reflex cycle implies association of sensation to movement; and, further, we see that this association is adapted to a particular end. Our conscious voluntary acts come under this definition. Equilibrium in standing or in progression may be an act of this nature in an individual attacked by paralysis, or in whom the cerebellum is destroyed, who can supplement the absent mechanism by efforts of reason; in the infant who learns to hold himself upright and to walk; even in the individual who, in order to accomplish a difficult equilibrium, puts his brain to work so as to assist his cerebellum. But these are all cerebral acts; the action of the cerebellum is *automatic*, that is to say, without participation of distinct consciousness or personal will. In being constituted a functional differentiated system, the cerebellum has certainly acquired special aptitudes, from the point of view of sensibility as well as from that of motricity; only, being lost in the domain of unconsciousness, the former elude our observation even more completely than do the latter.

4. Sources of stimulation.—Thus we see that, in order to bring about the motor effect by which equilibrium is ensured, the cerebellum gathers impulses from several senses. In the first place it receives them through the *vestibular nerve* from a special apparatus annexed to the sense of hearing: the *semi-circular canals*. Flourens was the first to observe the extremely strict functional relationship existing between this apparatus and the cerebellum. Lesions of the semi-circular canals give rise to the same disturbances as do those of the cerebellum; according as to whether one or the other canal be injured, disorders of equilibrium, rotation in one direction or the other, or in different directions, are produced, just as in removal of the unsymmetrical portions of the cerebellum. It is thence that the individual obtains his images of the *cephalic attitude*, which are due to the analyses effected by the ampullary nerve of the internal ear.

The cerebellum, on the other hand, receives impulses from two important senses, the *visual* and the *tactile* sense: from the latter it receives both superficial and deep impulses, especially deep ones coming to it from the muscles and the articulations themselves. These furnish the individual with the images of his *segmentary attitudes*. Thus in man, when in the upright position, the reciprocal attitude of the foot and the leg play an important part (and especially when the ampullary images are disturbed). From this results what might be called a new

sense, taking cognizance of the oscillations of the leg on the foot and permitting the tibio-tarsal muscles to accomplish definite efforts for the correction of errors of equilibrium directly these show a tendency to arise (Bonnier).

5. **Progress of the impulses.**—The cerebellum, like the spinal cord and the bulb, is capable of reflecting the impulses coming to it from the organs of sense on those of movement ; it is in fact attached to the spinal cord by two kinds of fibres, the first ascending (direct cerebellar tract), and the second descending, which it associates by its grey substance, having special functions in view (equilibrium), which may be exercised without the intervention of consciousness. But, further, and in this once more resembling the spinal cord and the medulla oblongata, the cerebellum is located in the course of a general current of impulses, which passes through the brain. In fact, we see it connected with the optic thalamus and the cortex by the superior cerebellar peduncles, which allow of its exchanging impulses with these organs.

The sensory impulses of bulbo-medullary origin may then go beyond it, and may reach in the brain : (1) the optic thalamus, (2) the cortex. From these two collections of grey matter we know that they may again descend to the grey bulbo-medullary axis by the crura cerebri : this seems to be the most probable path. We have no reason to think that this path is an exclusive one, and on the other hand, we know that it is not simple. The fibres of the pyramidal tract (that is to say, motor) descending from the cortex give off collaterals when passing through the pons, which become connected with the fibres of the middle peduncle, and proceed to the cerebellum. This distribution of descending impulses on the path of the same fibre which furnishes them in this way both to the cerebellum and the grey bulbo-medullary axis simultaneously, is a detail of structure the part played by which still remains unexplained. On the other hand, the crura cerebri contain ascending elements (that is to say, sensory) which proceed to the optic thalamus and to the cortex (thalamic and cortical portion of the fillet) (*ruban de Reil*) ; and from these areas of grey matter the impulses find paths for returning to the brain by the superior peduncles of the cerebellum. From the cerebellum they have once more efferent paths to bring them back to the spinal cord by the inferior and middle peduncles.

Anatomy, by its special methods, shows us that the impulse may be propagated in both directions (afferent and efferent fibres), in each of the three peduncles which on both sides attach the cerebellum to the adjacent masses both above and below. From this results the possibility of the existence of cycles whose general direction varies sometimes in one way, sometimes in the other, and which may give rise to

currents capable of being inverted or even of co-existing, according to circumstances, since conducting elements, at once opposed and independent, exist in each of the three peduncles.

The cerebellum and reflex movements.—The cerebellum maintains equilibrium We recognize that it exerts an action on the muscular tone: and, in the same order of ideas, we also attribute to it a part in the execution of a great number of reflex movements which, according to some authors, would without it become impossible, at least in man (Bastian). Certain pathological facts have been appealed to in favour of this influence of the cerebellum on reflex actions.

As a result of compression, destruction and interruption of continuity of the dorsal spinal cord, the tendon reflexes will be seen to disappear (flaccid paralysis): following injuries which involve the cerebral hemisphere or its white tracts above the pons, an exaggeration of these reflexes will be observable (posthemiplegic contraction). Van Gehuchten explains these clinical differences by the varying site of the lesion, which, in the case of medullary injury, suppresses the influence of the cerebellum, and in that of cerebral lesion allows of its persistence.

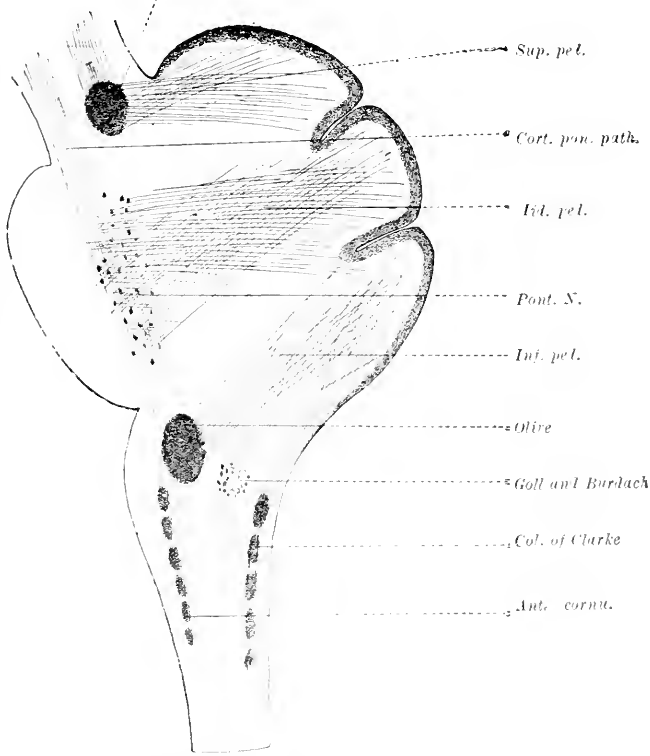


Fig. 152.—Diagram of the connexions between the cerebellum, the brain, the pons and the spinal cord (Charpy).

Yet more, in this latter case these reflexes are often exaggerated: thus the brain, in addition to the motor or exciting action that it certainly exercises on the spinal cord (cortico-spinal fibres), also possesses another, of inhibitory nature, which affects the cerebellum (cortico-ponto-cerebellar fibres).

The disappearance of this arresting influence, in the case of cerebral destruction would, in spite of the deficiency of cerebral exciting action, still be sufficient to give to the cerebellum a preponderating influence in the excitation of the spinal cord by its descending fibres (cerebellar-spinal).

Red nucleus.—Van Gehuchten, on the other hand, draws a distinction between the tendon reflexes (having for starting point mechanical stimulation of a tendon) and cutaneous reflexes (produced by irritation of the skin). According to this author, the latter are developed in an arch completed in the cortex, and they depend on the integrity of the *cortico-spinal* path; the former are developed in an arc completed in the red nucleus, they are connected with the integrity of the *rubro-spinal* path; on the tendon reflexes the cortico-spinal path exercises an influence which is for the most part inhibitory.

Medullary reflexes.—After section of the spinal cord (for example, in the dorsal region), the possibility of eliciting reflex movements of the inferior limbs will not have entirely disappeared, even in man, where it is less than in animals; but,

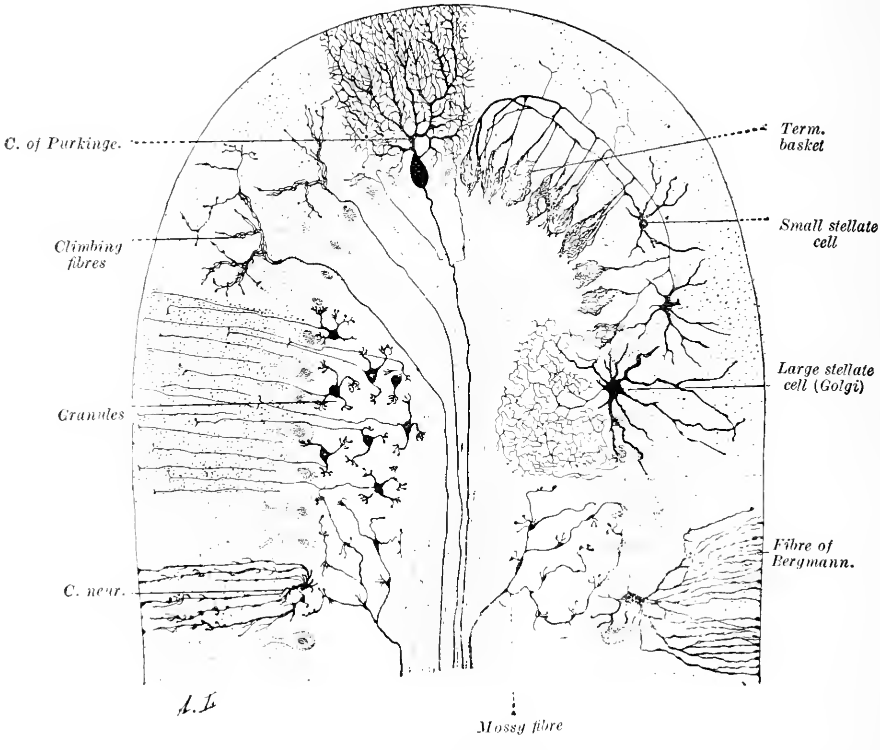


FIG. 153.—Structure of the cerebellar cortex.

Section of a convolution. Diagram after Cajal, slightly modified. The cell of Purkinje is seen from the front.

according to the preceding authors, these reflexes are not the normal equivalents of those aroused by stimulation of the skin or of a tendon in a healthy individual, or even in one attacked by cerebral lesions. They retain their interest from the point of view of the general physiology of the nervous centres; they have no diagnostic value with regard to the seat of mesencephalic or medullary cerebral alterations.

ANATOMICAL DATA.—The cortex of the cerebellum is formed of two superposed layers, one of grey (*molecular layer*), the other of a yellowish aspect (*granulated layer*). Between their boundaries are situated the cells of Purkinje, whose dendritic prolongations extend in the first, while their axis-cylinder prolongation

passes through the second. These elements are still more characteristic of the cerebellar cortex than are the pyramidal cells of that of the brain.

Cells of Purkinje.—These cells have more analogy than one with those of the second layer of the brain. Their body is surmounted by a plume of dendrites which extends by free ramifications into the molecular layer, and is continued in the deep portion by an axis cylinder, which is lost in the medullary substance ; this axis cylinder throws out collaterals which re-ascend into the molecular layer, as though to come into contact with the dendrites of the neighbouring cells. Do they receive or do they distribute impulses in this locality ? Once more we find ourselves confronted by this question which experiment has left unanswered. It seems rather as if the impulses running off by the axis cylinder, in the direction which is called cellulifugal, must partly leave it by these collaterals, and by them be secondarily propagated to neighbouring cells, which thus are associated in function with the cell receiving the initial impulse. There would in this way be not only cells (short neurons) of association, but, in the true sense of the word, fibres (prolongations) of association, thrown between neurons of the same nature

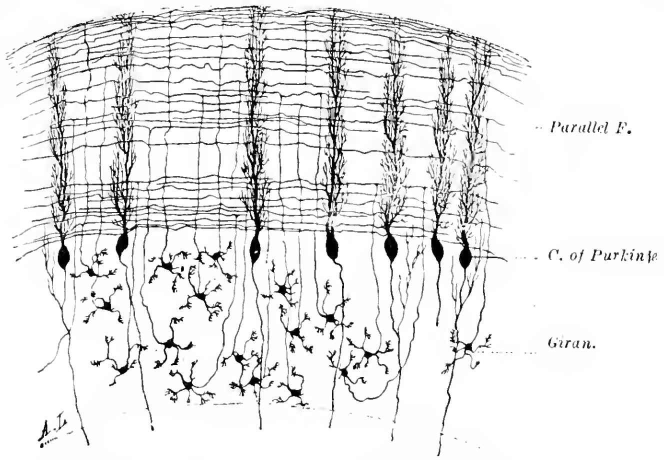


FIG. 154.—Structure of the cerebellar cortex.

Frontal section of a convolution, after Kölliker.—The cells of Purkinje are seen in profile and the parallel fibres from the front.

as are these latter ; the pyramidal cells of the brain, and the cells of the anterior horns of the spinal cord show, on the other hand, a similar arrangement.

The cells of Purkinje are obviously elements which conduct the impulse away from the cerebellum, after having received it therein. It is not known to what nervous organ they transmit it ; their analogy of form with the pyramidal cells of the cerebral cortex would tend to show their connexion with the spinal cord.

Climbing fibres and mossy fibres.—As counterpart to the cells of Purkinje, axis-cylinder terminations will be found in the cortex of the cerebellum which, in an equally obvious manner, carry to it impulses coming from elsewhere : these are the *climbing fibres* which terminate in the molecular layer by rolling their arborizations around the dendritic prolongations of the cells of Purkinje, and the *mossy fibres* which terminate in the granular layer around the cells belonging to it (the granules).

On the other hand, we know that the cerebellum is united to its adjacent organs below (spinal cord, medulla oblongata, pons) and above (cerebral cortex, optic thalamus) by its three double peduncles, not to speak of its own nuclei (corpus dentatum, nucleus of the roof) and the connexions which either these bodies, or

its cortex, contract with masses of lesser importance, such as the red nucleus (above) and the bulbar olive (below). It is very difficult to ascertain exactly which of the preceding elements (which we can only call *cerebellifugal* and *cerebellipetal*), serve to effect such and such of these numerous connexions.[1]

Cells of association.—The cells of association are distributed, some in the molecular layer, and others in the granular layer.

Molecular layer.—It contains *stellate cells* of small volume. The short rays of these cells seem to be those which receive the impulses. On the contrary, two of these rays, situated in each other's prolongations, form a double axis cylinder extending for a certain distance in two opposite directions. Their orientation is remarkable; they are situated in the plane which contains the plumes of the cells of Purkinje, and consequently perpendicularly to the direction of the layers and tangential to these layers. At the level of each cell of Purkinje a collateral is detached, which furnishes around the body of this cell a veritable network, enclosing it with its free ramifications, like a sort of *basket*, whose very narrow opening, closed on the cell, allows its axis cylinder to pass through.

The cells of Purkinje are thus mutually associated, in the direction of the thickness of the layers.

Granular layer.—Subjacent to the preceding, this layer contains small *polyhedral cells* (the *granules*) which repeat, under new forms and arrangements, the preceding associating disposition. Furnished with short dendritic prolongations by means of which they receive the impulse, these cells give out an axis cylinder which at first follows an ascending axial direction in order to reach the molecular layer: once there, it bifurcates to right and to left and becomes tangential; its orientation is in the same direction as the layers which it follows from one end to the other, and is consequently perpendicular to all the preceding (*parallel fibre* of Cajal).

It gives off no collateral, but traverses all the plumes of the cells of Purkinje perpendicularly to their plane and thus connects these cells in the direction of the layers, as they are already connected perpendicularly to this direction. One variety only of cells does not conform to these more or less geometrical types; these are the large stellate cells, whose ramifications, both those of the axis cylinder and protoplasmic, proceed in all directions.

Connexions of the Cerebullum studied according to the method of degeneration

A. Hemisection of the spinal cord.—a. *Ascending and descending degeneration in the spinal cord.*—(1) In the posterior columns (descending and of slight extent); (2) In the direct cerebellar tract (the whole extent in both directions); (3) In the anterior columns (two directions and rather far); (4) In the lateral columns (two directions, but near the section).

b. *Degeneration in the cerebellum.*—Degeneration of the periphery of the lateral column going to the cerebellum; direct course without decussation as regards most of the fibres; it passes into the restiform body, into the dorsal convolutions of the vermis; two other tracts going to the vermis or to the median nuclei of the cerebellum.

B. Lesions of the cerebellum.—*Descending degeneration.*—(1) Short path of association (corresponding side); short commissural path (opposite side). (2) Long crossed path; a small portion for the acoustic field of Ahlborn; a

[1] This example shows clearly how fundamentally indefinite are the designations of *centrifugal* and *centripetal*, of *motor* and *sensory*, so often applied to neurons having no immediate relation with the periphery. The cerebellum is an important centre, but this centre is subordinate to the brain and the fibres uniting the one to the other in two contrary directions, leaving one centre in order to attain another, are all of them simultaneously centrifugal and centripetal. For fibres of association uniting equivalent regions of the cortex of the brain, the unsuitability of the terms above designated is still more evident.

larger portion passes by the posterior (inferior) cerebellar peduncle into the medulla oblongata and the lateral column of the spinal cord; nothing in the telecephalon and the mesencephalon.

In order to elucidate the function of the cerebellum there are two methods of procedure: the one consists in separating it from its natural connexions, by cutting its peduncles separately; the other in dealing directly with it, by slicing it in a methodical manner, or else by stimulating it.

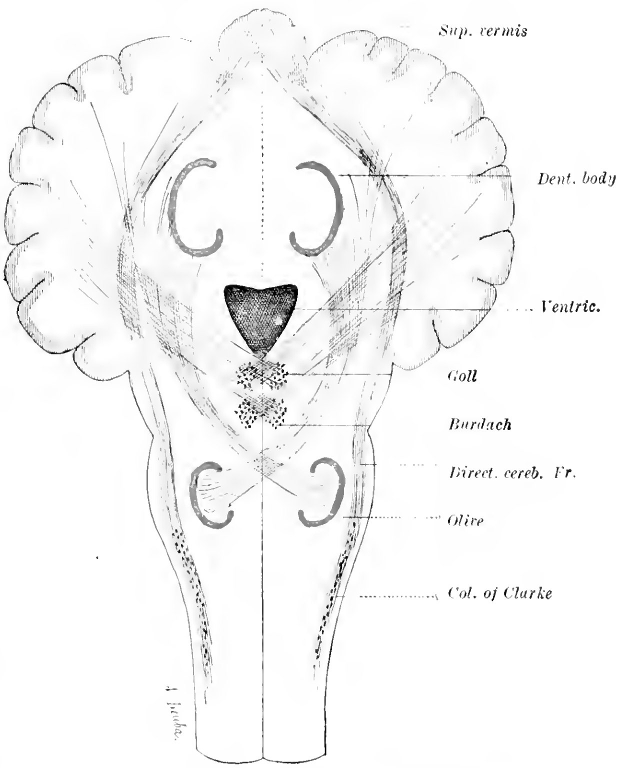


FIG. 155.—Diagram of the inferior cerebellar peduncles (Charpy).

2. Experimental data and those yielded by observation

A. CEREBELLAR PEDUNCLES.—The cerebellum is attached to the spinal cord, the medulla oblongata, and to the brain, by six peduncles (two for each). They are all formed of fibres which may be described some as *afferent*, and others as *efferent* with regard to the cerebellum itself; their mutual proportion varies according to the peduncles.

1. **Inferior cerebellar peduncles.**—They contain fibres which arise: (*a*) from the column of Clarke (by the direct cerebellar tract of the spinal cord); (*b*) from the nuclei of Goll and of Burdach (arciform fibres); (*c*) nuclei of the auditory, trigeminal, glosso-pharyngeal and vagus (sensorial tract going to the nucleus of the roof); finally (*d*) from the bulbar olivary body, which draws them itself from the spinal cord, with the grey matter of which it seems to be united in a twofold manner. All these fibres are grouped in the inferior peduncle of the

cerebellum which, in the neighbourhood of the medulla oblongata and the spinal cord, takes the name of *restiform body*, and whose fibres, in this locality partly curved, are called *arciform fibres.* Amongst the efferent fibres, one portion turns aside to pass through the middle peduncle. The efferent fibres mixed with others reach the nuclei of the bulb and the anterior horns of the grey matter of the spinal cord, by the path of the anterior columns and the direct cerebellar tract.

Experiment.—Rolando and, later, Magendie have observed that section of the inferior cerebellar peduncle causes animals to assume a singular position, consisting of a *curving of the body into an arch* on the side of the wound. According to Longet, in order to produce this result it is necessary that the section should abrade the *intermediary tract* of the medulla oblongata subjacent to the restiform body.

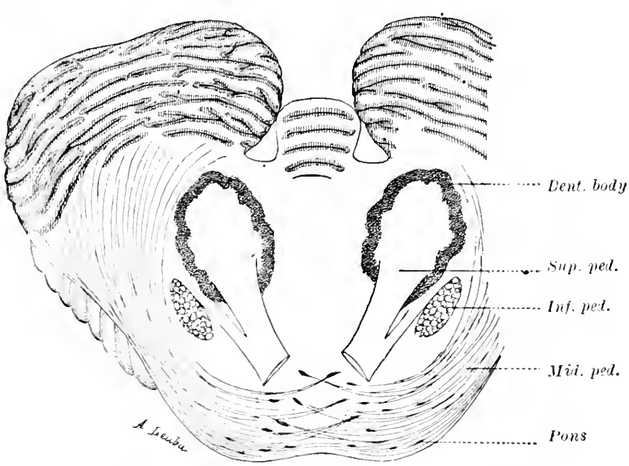


FIG. 156.—The middle cerebellar peduncles.
Horizontal section of the cerebellum.—Semi-diagrammatic figure (Charpy).

After section of the inferior cerebellar peduncles Flourens has noticed a *tendency to kicking*; this, however, is contested by Longet.

2. **Middle cerebellar peduncles.**—These unite the nuclei of the pons to the cortex of the cerebellum; they also contain *afferent* and *efferent* fibres and, in addition to these, *commissural* fibres mutually connecting the cerebellar hemispheres, and which therefore pass through the median line without interruption.

The nuclei of the pons (annular protuberance) are, in part, the continuation of the grey matter which is, in the medulla oblongata, the origin of the motor nerves and the termination of the sensory nerves. But, in the same way as in the medulla oblongata, special formations superadded to these nuclei are found in the thickness of the pons (in the interval between the white tracts which cross in it, following two principal directions. One of these duplicates the structure of the bulbar or inferior olive: this is *the pontine* or *superior olive.* Rudimentary in man, it is highly developed in certain animals, such as the

cetacea, the cat, the sheep (M. Duval). The others are nuclei of the pons properly so called, being more or less condensed or diffused grey masses contained in its substance.

All these formations are connected : (1) with the periphery by elements, partly centripetal and partly centrifugal, which they associate for the performance of reflex acts : (2) with the cerebellum by the ascending and descending fibres of the middle cerebellar peduncle, and with the brain by the collaterals of the pyramidal tract and the two cortico-pontine tracts. The nuclei of the pons become degenerated in cases of atrophy of the cerebellum (Pierret).

Experiment.—Section of the middle cerebellar peduncles produces pronounced *movements of rotation*, observed by Pourfour du Petit, rediscovered and described by Magendie and Flourens. These movements may also be observed after section of the pons Varoli when this is effected outside the median line ; and they are the more rapid in proportion as the section affects more especially the middle peduncles properly so called. Magendie has also noticed an extraordinary change in the position of the eyes, the one on the side of the lesion being turned downwards and forwards, and that of the opposite side upwards and backwards.

The movement of rotation is in this case a *rolling movement ;* it is sometimes effected with such rapidity that the animal may perform more than sixty revolutions in a minute. The direction of the movement varies according to the position of the section in the peduncle. According to Magendie, the rotation takes place from the side of the section. According to Longet and Schiff, this is so when the peduncle is attacked through the occipito-atloid space which has been laid bare, and when the middle peduncle is cut posteriorly. If the peduncle is cut or injured in front, the rotation is performed from the side opposite the section ; this is the most usual direction of the movement, and the one remarked in certain clinical observations. According to Schiff, this difference is due to the fact of the corresponding hemisphere of the cerebellum being injured in the latter case ; but Longet, who has undertaken a re-examination of the question, explains otherwise this difference in results. The section made posteriorly attacks the uncrossed fibres, while that in front affects fibres after decussation ; according to this author the movement would be made from the stronger towards the weaker side.

3. **Superior cerebellar peduncles.**—Also formed of efferent and afferent fibres, these peduncles extend along the front of the cerebellum, decussate below the corpora quadrigemina, and join the crus cerebri, being placed in its superior layer. After a more or less complete interruption

in the *red nucleus*, they continue their course towards the optic thalamus and the cerebral cortex.

Experiment.—Like that of the middle and inferior, irritation of the superior cerebellar peduncles gives rise to manifestations of sensibility (Longet). The movements or rotation are less easy to define on account of the large amount of destruction necessitated by an operation on these parts. Section of a superior peduncle produces an arched curve of the body on the injured side and circus movements.

Section of the *cura cerebri* has the same effect as that of the superior cerebellar peduncles, this no doubt arising from the very great difficulty of operating in an isolated manner on these tracts, which are in

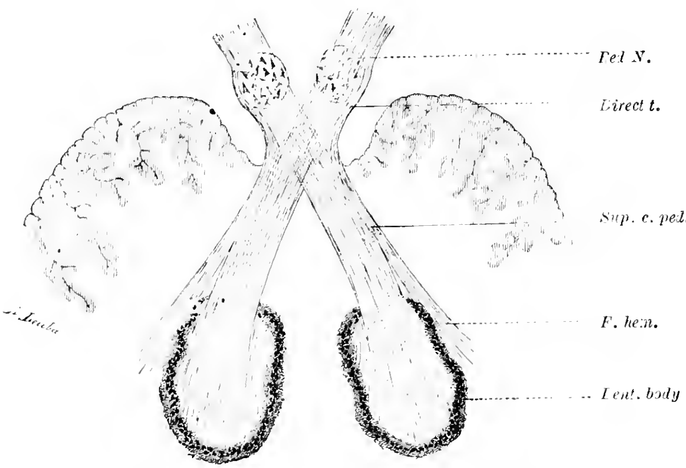


FIG. 157.—The superior cerebellar peduncles.
Origin and decussation (semi-diagrammatic figure) (Charpy).

such close vicinity as to become confused together. According to Longet, the circus movement is effected in the direction opposed to the side of the section.

4. **Olives and nuclei of the pons : their connexions.**—The bulbar olive is in strict developmental relationship with the dentate nucleus and the opposite lobe of the cerebellum ; atrophy of this lobe brings about that of the olivary body. Attached to the grey matter of the spinal cord, and also to the cerebellum, the olive is further connected with the brain by a tract which follows the crus cerebri in its tegmental portion (tract of the *calotte*), and is lost in the ne˙ghbourhood of the red nucleus belonging to the superior cerebellar peduncle.

Experiment.—The experimental destruction of the *bulbar olive* produces *disturbances of equilibrium* both in standing and walking (Bechterew). Its lesion in man produces vertigo, titubation and movement

laterally on the corresponding side; in fact, a true *pseudo-cerebellar syndrome* (Leclerq).

The bulbar and pontine olives and the nuclei of the pons are collections of grey matter which are very remarkable on account of the connexions they establish. They can exchange impulses with the periphery (centripetal and centrifugal) by the aid of the grey bulbo-medullary axis. With the cerebellum impulses can be exchanged by the afferent and efferent fibres of its inferior and middle peduncles, having for aim the establishment of a definite function, namely, equilibration. Finally (this we have already noted as regards the bulbar olive) they are connected with the brain.

The *pontine olive* receives impulses from the anterior nucleus of the *acoustic* nerve, and also from the acoustic striæ. It reflects these impulses on the nucleus of the *sixth nerve*, with which it is in relation, and furnishes them to the cerebellum, with which it is also connected.

The *nuclei of the pons* can exchange impulses with the cerebellum by afferent and efferent fibres. These same nuclei receive fibres descending from the cortex, *cortico-pontine* fibres, distributed in two tracts (*anterior cortico-pontine tract*, coming from the frontal lobe, and *posterior cortico-pontine tract*, coming from the temporal lobe). The nuclei of the pons have also with the cortex a connexion of a special nature: the pyramidal tract skirts along them and gives off to them numerous collaterals. These connexions with the cortex form the path which is called *cortico-ponto-cerebellar*.

5. **Movements of rotation.**—These may be produced by unilateral lesion of a fairly large number of portions of the nervous system. Vulpian gives the following enumeration of these parts: the cerebral hemispheres, the corpora striata, the optic thalami, the crura cerebri, the pons Varolii, the corpora quadrigemina and bigemina, the cerebellar peduncles (and specially the middle), and the lateral parts of the cerebellum, the olivary bodies, the restiform bodies, the external portion of the anterior pyramids (Magendie), the portion of the medulla oblongata in which the facial nerve arises (Brown-Séquard), the optic nerves, the semi-circular canals (Flourens), the auditory nerve (Brown-Séquard).

Generalization.—These movements may be observed in all vertebrata; they may be elicited in the frog and in fish. In these a unilateral lesion of the isthmus of the encephalon causes a rotation of the body round its axis, which is less rapid than in mammals.

Classification.—These movements differ from each other according to the situation of the portion of the nervous system which has been injured. They may be classed under three headings: *movements of*

rotation on the axis, like those of which we have just spoken ; *movements like the hand of a clock,* the axis of rotation perpendicular to the trunk passing through the posterior limbs ; *rotatory movements* (circus movements), in which the animal follows a circular tract.

Differences according to the injured part.—Lesion of an anterior portion of the encephalon, such as a hemisphere, would cause circus movements. In proportion as this injury approaches the pons, these movements change into the rotation resembling the hand of a clock, whether it be that the animal turns on its own hindquarters or whether the imaginary clock-hand prolonged behind the body has an axis (also imaginary) at a certain distance from it. Should the lesion attack the pons or the part representing it, a rolling movement is produced.

Frequent discussions have taken place between observers or experimenters concerning the determination of the direction of rotation with regard to the right or left side, according to which it is effected.

Rules for defining the direction of the movement.—Prevost observes that these discussions have usually as a starting point, not the divergent results of experiments or of observations, but the different conventional manner of defining the movement of the subject under observation, with regard to itself and also to the observer. This author shows that the *conjugated deviation of the eyes* and the change of position of the head accompanying it may serve to define the direction of these movements. Deviation of the eyes and head is often the starting point for movements of rotation by extension to the other muscles of the body. The relation of this deviation with regard to the lesion is easy to establish ; it is durable ; the deviation takes place from the side of the lesion.

If, for example, the cerebral injury is on the left, the eyes and the head are deviated to the left (with regard to the subject under observation). If a movement of rotation be produced, it will cause the body of the subject to turn as on a pivot in the same direction, from right to left with regard to itself. But if the subject falls on the ground with the face downward, and we observe it by placing ourselves at its feet, it will appear to roll from left to right (with regard to our own right and left), while in reality continuing the same movement. All descriptions of movements of rotation may be verified by recalling these definitions.

Paralytic and irritative lesions.—Clinical observations on conjugated deviation of the eyes and head further teach us that unsymmetrical movements or attitudes are due to paralysis of the injured parts, interrupted in their continuity, and to the predominance of action of the symmetrical nervous structures remaining intact. But further, in the course of cerebral affections of a paralytic nature occasioning these deviations, irritative lesions may take part which, like those observed by Landouzy and Grasset, may change their character (contractures, Jacksonian epilepsy). These attacks are of short duration, thus showing that the durable modifications of the attitude, or even the motor unsymmetrical tendencies resulting from it, are really of a paralytic nature.

Apart from the cases of simple deviation, the mechanism of these changes of position and that of the movements of rotation continues to be unknown and very obscure. Neither unilateral paralysis of conducting fibres or of centres duplicated in the nervous system (Lafargue), nor that of adductors of one side

coinciding with that of abductors of the other (Schiff), nor the suppression of restraining forces necessary to equilibrium (Magendie), nor, finally, inhibition at a distance, suffices completely to explain this mechanism.

B. Effects of destruction of the cerebellum.—Destruction of the cerebellum may be either *total* or *partial.* It may be directed to the *vermis* alone or to the whole. It may also bear upon half of the organ, the other half being respected. And, finally, it may in the vermis affect either its anterior or posterior portion. Flourens removed the cerebellum by successive slices, observing the disorders produced after each ablation.

Three orders of phenomena.—The primary effect is that of *stimulation.* This once dissipated, contrary effects, called those of *suppression,* appear, which may be traced to loss of the cerebellar function. But in the long run effects of *substitution* are manifested, which, developed by exercise and a sort of new education, more or less disguise the preceding results in spite of the lesion being irreparable. It is therefore

Fig. 158.—Attitude in repose, after destruction of the left half of the cerebellum (after Thomas).

difficult to maintain in a purely isolated condition either one or the other of these orders of phenomena. And authors also hesitate concerning the duration of each of these phases. Some, with Luciani, give great importance to the effects of irritation ; others, with Thomas, restrict them to the moment of operation (action of instruments, compression by clots of blood). The criterion, as regards their distinction, is to seek for the inversion of effects, which will be more marked in proportion to the length of time elapsed since the operation.

We will describe the effects of destruction of the cerebellum, taking as a guide the very circumstantial description given of it by Thomas.

1. Unilateral destruction.—Effects consecutive to the operation.—There is *conjugated deviation of the eyes* in the *direction opposite to that of the lesion,* combined with *nystagmus.* If placed upright, the animal falls *on the side of the lesion,* and rolls on the longitudinal axis of the body, this movement continuing. These movements are spontaneously reproduced with intervals of repose during the first days after

the operation, and also on the least irritation, painful, acoustic or tactile.

In repose, the animal is contracted, and lies on the side operated on, the head stretched out and thrown back towards the side of the lesion; the limbs (especially the anterior) are extended and more contracted on the side operated on. The trunk is inflected (pleurothotonos) with the concavity turned towards the lesion. This attitude is at first irresistible, and the animal returns to it when disturbed.

Amendment of the disorders.—After four or five days, amelioration of these disorders appears, and the animal endeavours to perform several movements. It can tolerate decubitus on the stomach, by keeping its limbs very widely separated. Up to this time the tendon reflexes are increased, but their increase then gives place to a *diminution of tonicity;* the increased reflexes are considered to be the effect of irritation.

Immediately after the operation the animal has *difficulty in swallowing*, so great that the act is almost impossible. This symptom quickly disappears, while the prehension of food, necessitating external adapted movements of the head, remains difficult for a long time on account of the oscillation of the latter.

After fifteen or twenty days, the animal can hold itself upright, maintaining its equilibrium on its widely stretched-out limbs. If it tries to raise a forepaw (generally that of the side operated on), this change of position is no longer effected by compensatory movements bringing back the axis of the centre of gravity within the base of support thus displaced and reduced: the animal falls heavily on the side of its cerebellar lesion. These phenomena during standing and walking are accompanied with trembling and oscillations of the body, which speedily bring about fatigue and accelerate the respiration. The muscles of the injured side seem feebler, and their movements are abruptly performed.

Little by little elevation of the anterior paw can be effected, then that of the hindquarters; walking and running become possible. These corrections are made by a new mechanism and by efforts of substitution on the part of organs: but movement is without suppleness, and has a rigid and intentional character, not shown in the ordinary purely automatic movements of walking in animals.

Simple equilibria independent of the cerebellum.—*Swimming,* on the contrary, becomes possible much sooner and more easily, because the conditions of equilibrium are here incomparably simpler than in walking. The position of the trunk in the water is not, however, symmetrical, the healthy side plunges more than the side operated on;

the head inclines slightly toward the healthy side; and progression is effected with slight deviation toward it.

Co-ordination and equilibration of medullary origin.—Tarchanoff has observed that, after decapitation (section of the spinal cord in the middle of the neck), a duck is able to preserve its equilibrium in the water, but not on the ground. The spinal cord of this bird contains associations which are sufficient to ensure regular movements for remaining upright in the water and for swimming, while standing on the ground and walking represent a much more complicated equilibrium, which requires the assistance of other associations (especially the cerebellum). Section of the neck and spinal cord causes an excitation which brings this mechanism into play for a short space of time. A fresh section provokes a fresh bout of swimming (and even of flight). An external stimulation has the same effect; or it may sometimes arrest the movement just beginning to be performed.

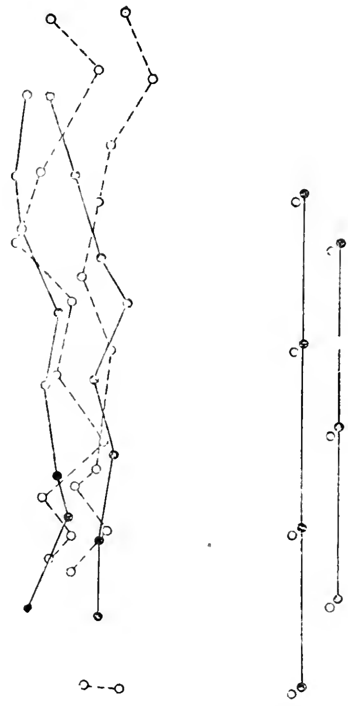


FIG. 159.—Tracing of the gait of a dog, after ablation of the left half of the cerebellum, taken at the period of restoration of function.

Fore paws in white; hind paws in black. On the right, tracing of normal gait (scale $\frac{1}{12}$). On the left tracing of the gait of dog operated on—exaggerated separation of the paws and irregular gait. Below, normal extent of the separation of the paws in a position of repose (after Thomas).

2. **Total destruction.**—As Vulpian and Schiff have remarked, total destruction of the cerebellum is followed by effects which are apparently much less serious than partial destruction affecting half of the organ. This may be understood with regard to an apparatus whose function is to preserve equilibrium by bringing bilateral forces into play, many of which are reciprocally antagonistic. But if the movements of rotation are suppressed, the effect resulting from this suppression is again displayed by disturbance in the position; the head is forcibly extended, the trunk is in opisthotonos, the limbs (especially the anterior) contracted, there is nystagmus; then, when the movements return, titubation, oscillations and trembling, as much and more than in partial destruction.

3. **Destruction of the vermis.**—Its effects resemble those of total destruction, but are more rapidly recovered from : antero-posterior movements of oscillation, and a tendency to kicking.

4. **Predominating direct action.**—In the brain it is the crossed action which predominates : in the cerebellum, on the contrary, it is the direct action. *Each cerebellar hemisphere exerts a bilateral action, but one which is predominant on the same side. Each half of the cerebellum has its principal connexions with the opposite cerebral hemisphere and with the half of the spinal cord of the same side* (Luciani).

In certain cases it has been observed that atrophy of a cerebellar hemisphere corresponds with that of the cerebral hemisphere of the

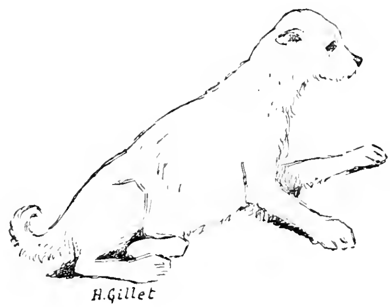


FIG. 160.—Attitude in repose, after total ablation of the cerebellum.

Period of restoration of the functions (after Thomas).

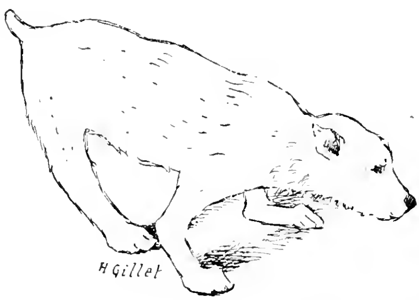


FIG. 161.—After destruction of the vermis.

Medium abduction of the anterior limbs. Abduction and projection of the posterior limbs (after Thomas).

opposite side. The superior cerebellar peduncles are very distinctly decussated as regards the larger portion of their fibres.

C. ELECTRIC STIMULATION OF THE CEREBELLUM.—Ferrier, after having exposed it, has stimulated the cerebellum in animals, and especially in the monkey.

a. *In animals.*—The results are as follows :—

(1) *Pyramid of the median lobe.*—The eyes move horizontally in the direction of the point of application of the electrodes.

(2) *Superior vermiform process.*

Posterior extremity.	*In the middle :*	The eyes look downward.
	On one side :	They look down on the same side.
Anterior extremity.	*In the middle :*	The eyes look upwards.
	On one side :	They look up and to the same side.

(3) *Lateral lobe.*—The eyes look up and from the stimulated lobe.

(4) *Flocculus.*—The eyes turn on their antero-posterior axes.

The head when left free is the seat of movements coinciding with those of the eyes : elevation, depression, etc. There is further a tendency to certain abrupt and intermittent movements of the upper limbs, and to extension of the legs on the side corresponding to the

stimulation. In the pigeon the head alone is displaced and not the eyes, and movements of the wing and the claw may be noticed. In fish the eye on the side stimulated protrudes, the tail is curved inwards on the same side, and the fins are spread out : if the stimulus is a median one, both eyes protrude and the tail curves upward.

b. *In man.*—Purkinje and, later, Hitzig, have stimulated the cerebellum in man by passing a galvanic current of medium intensity through it, the poles being respectively placed behind each ear, near the mastoid process.

The *subjective result* of this stimulation is a *sensation of vertigo*, characterized by an apparent displacement of objects in the direction of the current : from right to left, if the positive pole is to the right, or conversely.

The *motor result* is a depression of the head and the body on the side of the positive pole. This displacement of the head is also accompanied, as Hitzig has demonstrated, with *movements of the eyes* in the same direction, and often by *nystagmus*.

Remark.—In animals in which it is possible to uncover the cerebellum, stimulation is effected by placing the two poles on the region, or on the side of which it is intended that the activity should be manifested (bipolar stimulation). In man, where the electricity must penetrate through the bones of the skull, this mode of stimulation is not applicable, because, on account of the electrodes being too near together, the current would only penetrate the skin and not reach the deeper structures. It is forced to traverse (at least by a portion of its lines of flux) the intracranial organs to be stimulated, by placing the two poles on two symmetrical regions at the extremity of one of the diameters of the organ (in this case the transverse diameter). When it is remembered that the two poles have a very unequal stimulating value, the negative pole or cathode greatly preponderating over the positive pole or anode, the result is the same as if the stimulating current were applied only to the region where the cathode is placed (unipolar excitation).

1. **Agreement of the results.**—Hence it follows that the motor results of stimulation of the cerebellum in man are in unison with those obtained in animals. In both cases the eyes are directed to the side opposite to that which is being stimulated.

These results also agree with those obtained by symmetrical destruction. In fact, this destruction ought to have results contrary to those following excitation : and we have seen that it is followed by a displacement of the visual axis on the same side as the lesion, which is conformable to the logic of facts.

2. **Functional relations of the cerebellum and the brain.**—Luciani and Russell have studied the influence of cerebellar destructions (unilateral) on the excitability of the cerebral hemispheres. They agree in maintaining that this excitability is augmented in the hemisphere of the opposite side : it may also be increased in both hemispheres, but unequally (Luciani). Under the name of cerebral excitability is included the excitability of a complex system, beginning in the brain and terminating in the muscles, and of which the two principal segments, the brain and the spinal cord, has each its own special excitability, and may present, therefore, its own variations of this excitability. If we remember that the cerebellum is at the same time united to both of these two segments, we shall realize how uncertain and obscure is the mechanism of this hyper-excitability, without taking into account that it may be due to a phenomenon of evolution belonging to the functional compensation of cerebellar paralysis. In fact, as a result of ablation of a cerebellar hemisphere, an unusual development of the anterior portion of the brain, principally of the sigmoid gyrus, has been observed (Bianchi). However, Russell has noticed that this hyper-excitability exists almost immediately after the cerebellar lesion.

Antagonistic action.—The same author has studied the antagonistic actions of the cerebellar and cerebral hemispheres of the same side and the correlated actions of the opposite lobes. Simultaneous lesions of the cerebellar and cerebral areas of the same side may be combined in such a way as to leave the position of the eyeballs intact ; and the same may be said with regard to their excitation.

Inhibitory elements.—The existence of inhibitory elements in the cerebellum resembling those found in the brain has so far not been proved. In each case the search for these elements is surrounded with difficulties, on account of their being so closely blended with other elements whose function is opposed to them. At the same time it is probable that these elements exist in the cerebellum as well as in all the other deeply situated structures of the nervous system. It is a law universally recognized, that these elements are present in all the nerve tracts which connect the different regions of the grey matter with each other. All systems, however elementary, appear to contain them in conjunction with the elements excitatory of movement. The presence of these inhibitory elements seems to be a condition necessary to the balance of force in all these systems, as they regulate the excitations, and place them in equilibrium and also act as economizers of nervous force. Complex systems like the cerebellum and the brain may, in connexion with each other, play by turns the part of exciting or inhibitory agents according to circumstances ; but to neither does each function exclusively belong.

3. **Cerebellar vertigo.**—The sensation of vertigo which results from the artificial (electrical) stimulation of the cerebellum is a phenomenon of conscious sensibility which can hardly be explained except by the

fact that the cerebellar stimulation spreads to the cerebral cortex. The uncomfortable sensation caused by it very closely resembles the pain aroused by all sensory phenomena whose strength exceeds the normal (physiological) limits. It tends to prove that centripetal elements exist in the cerebellum, whose function it is to indicate to us the position of our bodies in relation to external objects. These centripetal elements exist in it conjointly with motor elements which act by maintaining the persistence of this position within certain limits.

Reflex cycle of equilibration.—Equilibrium in the upright position and in progression is the result of a reflex cycle, which connects these two kinds of elements: the first of these elements carries information to the cerebellum, which that organ, by means of the second elements, utilizes for the direction of the muscular contractions. This cyclic process, while confined to the cerebellum, is an unconscious one; that is to say, though it may be in some obscure way conscious in itself, it is situated outside the personal consciousness of the subject. When this process is extended so as to include the surface of the brain, it becomes, or may become, a conscious one, without the phenomenon ceasing to be normal, or, so to say, harmonic. The appearance of vertigo (as of all pain) is an indication of disorder and of functional loss of harmony: the sensory impulses are then giving us untrustworthy information with regard to the relations which exist between our bodies and the external world. In space the impulses penetrate the cycle in an abnormal manner at certain points of its course, instead of springing up regularly from their usual point of departure, so as to be renewed there, while circulating in it.

Reciprocal dependence of the sensory and motor elements.—As artificial stimulation of the cerebellum gives rise at the same time both to sensory and motor phenomena, it is reasonable to inquire whether one is the exciting cause of the other, and if so, which acts on which, or if both are elicited simultaneously. This last seems the most reasonable supposition. It is evident that the current which traverses the cerebellum does not distinguish between the sensory and motor elements which are there mixed together; and the somewhat strong stimulation which the current produces on these elements is by them transmitted to others, which diffuse it to a greater or less distance in different directions. The sensory elements, thus excited on their course, carry to the brain, and finally to the consciousness, erroneous information concerning the situation of the body, whether it be at the time in repose or in movement. This is what causes vertigo.

Vertigo, as is well known, arises when a rather rapid and prolonged rotatory movement is impressed on the body in a determinate direction, as, for instance, from right to left. When this movement ceases, objects appear to be displaced before the eyes in the opposite direction. If, while the body is in motion, the eyes are moved laterally in a contrary direction, or if at the moment when motion ceases they make this contrary movement as though to follow the apparent direction of the moving objects, then vertigo is diminished.

It is thus seen that vertigo is neutralized by the performance of one of the corrective movements which tend to re-establish equilibrium (or which gives the sensation of its re-establishment). It is the function of the cerebellum to secure these corrective movements by co-ordinating them with those of the primary movement.

Comparison of the functions of the brain and the cerebellum.—Compared with the functions of the brain properly so called (cerebral hemispheres), those of the cerebellum are specifically very different. This difference is demonstrated very

markedly by the experiments of Flourens, consisting in the removal either of the cerebral hemispheres, or of the cerebellum alone.

(a) *Removal of the cerebellum.—The animal deprived of the cerebellum, but retaining the brain, preserves unimpaired all its sensibility and all its spontaneity.* Once the shock of the operation over, it emits cries and is continually in movement (Luciani). It unsuccessfully endeavours to get up and walk, and gives signs of great uneasiness, thus showing that it *has retained its instincts and all its intelligence. It has in a way, for the moment, completely lost its function of equilibration ;* or, in other words, the faculty which it possessed of orientating the position of its body with regard to the direction of weight, either in an upright position or in progression.

(b) *Removal of the brain.—The animal deprived of the cerebral hemispheres, but retaining the cerebellum,* presents an entirely different aspect. *It has lost all clear consciousness* of what is passing around it, *and all spontaneity.* It remains motionless, does not avoid danger, neither seeks nor will take food even if placed in close proximity to it, and manifests neither instinct, intelligence, nor sensibility as generally understood. Yet *it has clearly preserved the faculty of equilibration.* The bird, after the removal of its brain, remains upright and motionless ; if thrown into the air, it extends its wings and sustains itself by their movements while falling to the earth. The voluntary impulsion is suppressed, but the automatic excitation which the movement gives rise to is performed regularly, until, having once more come into contact with the ground, the bird resumes its motionless position.

B. THE EMOTIONS : OPTIC THALAMUS AND CORPORA STRIATA

The impulses arising in the different senses find, at the base of the brain, a locality both for association and reflexion, whence proceed the sensori-motor phenomena which are called *emotional.* The connexion between sensation and movement is here direct and close, so that the motor reaction follows immediately on the impression ; this has caused the emotional phenomena to be compared to reflex acts. In this locality the sensations acquire a greater value and a more complete organization than in the grey bulbo-medullary axis ; their effective tone also is here very marked.

1. **Nervous reflex and conscious voluntary actions.**—The foundation of the classification of nervous sensori-motor actions is based on the contrast that may be drawn between reflex and conscious voluntary acts. In the first case the phenomenon of sensation is indistinguishable from the motor phenomenon, the answer to the stimulus is immediate ; the act is unconscious, automatic and performed in a mechanical manner. In the second case the two orders of phenomena are dissociated, and the answer to the excitation may be indefinitely deferred. The act is a conscious one, and as movement is not closely linked, either in time or space, to the immediate sentient impression, and as the relations have contracted great complexity, which appears to imply the fact of choice, the act may be termed a voluntary one.

2. **Emotional acts.**—The immediate connexion between movement

and sensation exists, or may exist, in emotion as it does in the reflex act ; for the motor reaction is often immediate and always involuntary. This reaction affects in a typical manner a greater or less number of the muscles, both of external and internal, or organic, life ; in this case the effect is a conscious one and produces a deep impression upon us. Emotion is sometimes called a *psycho-reflex* action, on account of its mixed character of involuntary consciousness.

Starting point.—The source, the point of departure of emotion, as in fact of all nervous action, is always external to ourselves ; it has two modes of origin, and the initial stimulus which produces it has also two ways of showing its effects. In the first it acts, so to speak, in a direct manner. In this case emotion is at once translated into motor action, which is assimilated to the mechanism of an ordinary reflex act. The second method is an indirect one, derived from an anterior excitation retained in the nervous system.

In other words, emotion may arise from a sudden impression (the sight of some object, the hearing of some sound . . .) ; it may also, on the contrary, be produced by an idea, a remembrance, or the sudden drawing together of two separate ideas which the brain's activity causes to unite.

External and internal interpretation.—Emotion is expressed externally by motor manifestations which reveal it to the eyes of those around. It is also echoed by the internal organs and the more important functions (respiration, circulation, excretion, etc.) ; when emotion is powerful it affects the whole being. This reverberation caused by emotional excitement on our internal organs is so prompt and so evident, that it has been made the pretext for locating the faculty of emotion in the organ most directly affected, that is to say, the heart. This theory, though frequently refuted, mistaking, as it obviously does, effect for cause, is continually finding supporters. Doubtless, if all the motor paths presiding over the internal and external changes by means of which emotion is revealed were interrupted, and if the secondary effects of these changes were wanting, the series of phenomena would be disturbed and emotion probably lessened. But as long as the principal associations from which these motor effects take their origin subsist in the deep masses of the nervous system, emotion remains possible.

It is principally the subject of the circulatory modifications accompanying the emotions which has caused the theory of their extra-cerebral situation to be formulated. The brain, like every other organ, is dependent on the circulation. Deprived of blood, it ceases to perform its functions. Taking this easily verified fact as a point of departure, some have supposed that the brain passively submits

to the oscillations of the general pressure, and that its activity follows these oscillations, whose rebound it cannot avoid. The *primum movens* of emotional reaction would thus be, not in the brain, but in the circulatory system, and the former would only translate it into motor action by its own particular kind of activity. This theory is unsound at every point. The brain, like every other organ, depends on the circulation; but, in this point also resembling every other organ, it has regulating cycles at its disposal which adjust the circulation to its requirements. Sensory nerves proceed from the surface of its arteries to the spinal cord and medulla oblongata, where the vaso-motor centres are situated. From these centres, by which it is reflected, the excitation returns to the arteries by means of a double system of constricting and dilating nerves contained in the great sympathetic. Resembling that of all other organs, the activity of the brain, by means of this mechanism of reflex and unconscious nature, controls its own circulation instead of being controlled by it. Not only does it govern its own circulation, but it also has the power of controlling the nervous bulbo-medullary centres, and through these the circulation of other organs. Further, it regulates, by parallel influences, the special activity appertaining to these organs. The impulses which at any given time descend from the brain to these centres acquire an exceptional intensity in strong emotions, and reveal them by the temporary disorder of these activities. Such is the succession of these phenomena.

1. Affective tone: pleasure and pain

The emotions are in themselves very diverse. They may be divided into two classes, according to the affective tone to which they respond. The first class answers to the call of *joy* or *pleasure*, the second to the note of *sadness* or *pain*. The first (pleasurable emotions) are accompanied by an increased bracing of the voluntary muscles, an augmentation of the respiration, a vaso-dilatation of the cutaneous peripheral system and a more vigorous heart's action. The second (emotions of sadness) are attended with a disturbance of the innervation of the voluntary and visceral muscles, a cutaneous vaso-constriction, and a diminution of the amplitude of the heart's action. In each of these two classes emotion manifests numerous gradations, and is sometimes inconsistent. In certain subjects this inconsistency is carried so far that the affective tone may be suddenly overthrown by it, and sometimes in violent emotion the manifestations proper to each condition may be partially intermingled (laughter ending in tears).

Being provoked by different and special exciting causes, our sensations are in themselves different and specialized, the specificity of each sensation being connected with that of the exciting cause by which the sensation is produced. And it will be seen that this arrangement is necessary in order that we may have information concerning all that exists and occurs around us. But this being so, it must be recognized that each sensation has two kinds of existence. One is of an *agreeable* nature, that is to say, pleasurable; the other *disagreeable*, that is to say, painful. It rarely happens that a sensation is one of absolute

indifference to us, in spite of appearances to the contrary. Over and above its original specific nature, each sensation has an *affective tone* in ourselves, which appears to have no purely physical origin.

1. **The connexion of the emotions with different kinds of sensation.**—Pleasure and pain affect not only the distinct and highly differentiated sensations which are at the foundation of our external relations (in the senses properly so called), but also those obscure, profound and latent ones (cœnesthesias), which rule in a harmonious manner the internal relations of our organs in the consensus which determines their functions. They obviously affect those which subserve nutrition. It is thus that hunger, thirst, and that need of oxygen which has no special name in ordinary language, seeing that we obtain this necessity of respiration without being forced to struggle for it, are affective conditions, to be classed under the heading of pain, just as their opposites. being conditions of need in a state of satisfaction, would be classified as pleasure. Fatigue, vertigo, chilliness, disgust, etc., are states of being of the same nature.

2. **Determinative condition.**—Pleasure and pain have this characteristic in common, that they do not develop themselves or attain their greatest intensity except by repetition or *summation* of the excitations ; it is in the sense of pain, however, that this determinative condition is chiefly manifest. It is by a summation of this sort that the muscular, articular, tendinous and visceral sensibilities are enabled to reach the threshold of consciousness, below which they are normally located, and to become of a really painful nature.

Transition from pleasure to pain.—In the senses, properly so-called, it is known that the slightest changes in the intensity of the exciting cause, or simply the persistency of its action, may bring about an easy and often rapid transition from a state of pleasure to one of pain. It is also known that the fact of summation, which is at the basis of these two conditions, is equally displayed by *the persistence of the agreeable sensation*, and even more so *by the continuance of the painful one, after the removal of the exciting cause.*

Relationship with the psychical functions.—The intensity of these two conditions, as regards equal exciting causes, varies greatly according to species, race, and the individual. Richet declares that pain is notably " an intellectual function which becomes more perfect as the intelligence is more developed." It is of small extent in idiots and insane persons. Its intensity is in proportion to the associations capable of being realized in the nervous system, and, above all, in the cerebral cortex. Pain survives in the memory in an acute, that is to say conscious, state for a certain time after its exciting cause is removed. Anæsthetics, by destroying the systematic associations which preside over it, prevent pain rom arriving at the threshold of consciousness, or perhaps hinder if from

dwelling in the memory ; either result is interpreted by us as a proof of its non-existence.

Pain is the internal revelation of functional disorder. It arises from any cause which tends to the disorganization of the elements, the tissues, or the systems composing the economy. It is for this reason one of the most habitual and constant symptoms of pathological states, conditions in which the life of the individual, or that of his component organs, is not undermined, but threatened. The more or less violent motor reactions to which pain gives birth are essentially defensive ones and appropriate in a greater or less degree to fulfil their conservative intention.

3. **Non-specific nature.**—*Pain is not, therefore, connected with any special exciting cause, but appears as the consequence of every excitation which, by its intensity or its abnormal repetition, transgresses the conditions requisite for the maintenance of the functions in good order.* From this it follows that pain requires no special apparatus for its production. There is no organ of special pain sense, and there are no special conductors of pain (there are no pain nerves). There is no system which properly belongs to it (no region in the cerebral cortex which is allotted to it). Further, there is no localization, using the word in its ordinary sense, for the sensitive and sensorial functions properly so called. It is true that all pain is not alike : it may be described as cutting, burning, pricking, tearing, acute, dull, etc. : all these terms recall more or less the mode of action of the abnormal excitants, capable of producing it experimentally, and which are connected with the variations of the traumatism which produces the excitation.

4. **Habitual field of action.**—As the surface of reception afforded by the area of touch is incomparably larger than that of the other special senses, and as this surface comprises that of the mucous membranes, and also, by gradation, that of the parenchyma of all the somatic or visceral organs, pain has incomparably more frequent opportunities of arising in the field of tactile sensation than in that of the other senses. Practically it is here alone that pain offers itself to observation with the characteristics which we are accustomed to recognize in it.

5. **Stimulation of nerve trunks.**—Pain may have its origin in intense and more or less destructive irritations, not only of the receptive apparatus of the senses, but also of those of the nerve trunks, which directly take their origin in these apparatus (compression, section, puncture, electrization, burning, and different mechanical and chemical actions. . .).

The action of electricity, so often employed as an excitant in physiological

practice, is the one most compatible with the preservation of the organization of all tissues and functions which it presides over. Nevertheless, it produces some slight alterations (electrolytic, for example), but these are quickly reparable on the cessation of the passage of the currents. It is this fact which causes electricity to occupy a place by itself amongst analytical reagents used by the physiologist. All excitants of whatever nature, including the electric current, when applied to a sensitive part, usually show the reality of their effect by pain. We may, therefore, reasonably consider pain to be an increased manifestation of tactile or general susceptibility. The functions of the sensory nerves, and especially of their posterior roots, have been studied according to the effects which result from their stimulation; these effects being not simply tactile, but also certainly painful.

Irritation of the great sympathetic may, by repetition and the summation which is the consequence of it, give rise to pain of a specially dull nature.

6. **Stimulation of the central masses.**—Painful sensations may be caused not only by irritations brought to bear on the sensitive neurons of the periphery, but also by those which reach the ascending neurons of the deeper systems. In this class may be placed the experimental excitations which may be localized on the endogenous tracts of the spinal cord and medulla oblongata. Certain clinical observations tend to the same conclusion : foci of hæmorrhage or of softening may sometimes cause great suffering when situated in the optic thalamus, the fillet (*ruban de Reil*), or the internal capsule (Edinger). Nevertheless, lesions of the encephalic masses do not present the phenomenon of pain to a degree equal to that shown by lesions of the spinal cord. It is a remarkable fact that in this point lesions of the cortex yield precedence both to the spinal cord and to the optic thalamus, and especially to lesions of the nerve trunks.

7. **Stimulation of the cerebral cortex.**—Cephalalgia, so frequently observed, is a pain which it is impossible to clearly localize. The brain is surrounded with membranes, of which one especially, the *dura-mater*, has been found *sensitive* to experimentation. Further, in this membrane the existence has been proved, not only of nerve fibres, but also of sensory receptive apparatus resembling those of the sensitive membranes. Experimentalists accustomed to practise stimulation of the cerebral cortex have not noticed, as an effect of these stimulations, the sharp pain which follows that of the posterior roots, while they have observed that these stimulations, when directed to certain determinate points, give rise to definite movements. Therefore we infer from this that *the organ which is usually considered to be the seat of sensation, viz. the cerebral cortex, shows no sensibility when the stimulation bears directly on itself.* This result, which seems startling at first sight, will cease to cause surprise if we take into consideration the fact that the stimulus thus supplied to the cortex is totally different from that

which reaches it normally from the sensory nerves through the medium of the spinal cord and its superior prolongations.

Development in the field of sensation.—It is not merely the cerebral cortex, the optic thalamus and the spinal cord which cause sensation to become a reality, making it, above all, actual, intense and painful; it is rather the whole formed by these parts which transmits the impulse in a determinate order, conferring on it at each fresh halting-place a character which it did not possess before arriving there, this character, however, having been elaborated at the previous stopping place. The further we recede from the cortex and the brain to obtain a starting point for the initial shock we are about to provoke, in other words, the further we encroach on the nervous system to launch the impulse which is intended to reach the cortex, so much the more complete will be the sensory effects of this impulse, as experiment shows us and as is also easy to understand. The comparison of the avalanche, inaccurate as applied to the elementary conductors (nerve fibre), becomes an accurate one when we apply it to the field of sensation, with its associations of superposed elements, its numerous channels of dispersion, and its complications of all kinds. In the field of movement the phenomenon is exactly the contrary; here we find reduction and concentration of the excitation on one extremely simple organ, viz. the muscle.

2. Expression of the emotions

1. **Language of the emotions.**—In man the expression of ideas is conveyed by conventional signs and acquired voluntary movements. There is, on the other hand, an expression of the emotions by involuntary movements, constituting a kind of unlearnt universal language; this language exists from birth, and is found even in those animals whose organization approaches our own, principally the domestic animals. The language of the emotions responds to a double utility and even to a double necessity. It establishes a preliminary social link between animals of the same species, which enables them to recognize the internal condition of others, at the same time imparting knowledge concerning their own.

Moreover, the movements, both external and internal, aroused by emotion, although they may not possess the signification of a natural language, play, for the individual himself, a part both of defence and preservation. A violent emotion arranges beforehand the muscles and the limbs in a position suitable either for attack or defence.

Active and passive emotions.—Whether the establishment of a relationship between similar beings is in question, or merely the preservation of the individual, the apparently irrational movements which emotion gives rise to are in reality adapted to the necessities of each particular case. For instance, in the emotions which have a bearing on the struggle for existence the animal, in order to escape from the danger by which it is menaced, will strive to arouse a feeling in its adversary which would cause the latter to keep aloof; or it will strive as much as possible to conceal itself from the sight of its enemy. The elevation of the voice, the horripilation, the elevation of the corners of the mouth to display the teeth and their grinding, all these are means which come under the first

heading and show *active* emotion. The holding of the breath, and the mimicry which gives to animals the colour of the soil or of the vegetation amongst which they live, are means which come under the second heading, and may be considered as associated with *passive* emotions. In the conditions by which the perpetuation of the species is assured, means of the same kind are to be found; with this difference, however, that, in addition to attitudes and expressions suitable for the driving away of the enemy, there are others appropriate to the drawing together of the sexes: suggestive sounds of the voice, the songs of birds, and the brilliancy of plumage are all means of this description. In the more or less elementary social life observable amongst certain kinds of animals, the expression of emotion, communicated between individuals, has a common preservation for its aim. Thus, the cry of fright given by one acts as warning of the presence of danger to the rest.

2. **Innateness of the emotional mechanisms.**—The nervous associations which the mechanisms adapted to the expression of each particular emotion display, are innate in animals. They are transmitted by *heredity*, and differ therefore greatly from those acquired by education, these latter being the basis of language properly so called. Darwin, in seeking the laws of these associations, refers them to the three following principles. These principles, though throwing but a feeble light on the question, form the first sketch of a rational explanation of the emotional movements which has yet been attempted.

(1) *Principle of the association of useful habits.*—Movements which in man (and sometimes in domestic animals) now appear to be of not the slightest utility are continued in both by heredity, on account of an anterior utility which has disappeared owing to the present conditions of existence. Thus the blinking of the eyes and the agitation of an aching limb have been originally, and are still occasionally, movements useful for the avoidance of an annoying or painful excitation. These movements express, by symbolism and by habit, emotions analogous to those by which they were originally instigated. Further, the conventions of civilized life oblige us to restrain the manifestations of our emotions, but this restraint is incomplete and allows the involuntary revelation of our internal sentiments to transpire more or less distinctly, and thus the faintest indications of this nature become very expressive.

(2) *Principle of antithesis.*—If any given movement symbolizes a certain emotion, it is natural that the contrary movement should be chosen to signify the opposite emotion. A dog, imagining that he sees a stranger, immediately assumes a hostile attitude, shown by the stiffening of his limbs and the erection of his body and head. If in this stranger he suddenly recognizes his master, the expression of what he then feels is shown in a precisely opposite manner: in this case by a crouching attitude, and expressive movements of the limbs, more especially of the tail.

(3) *Principle of direct action of the nervous system.*—It would be more correct to call this the *overflowing excitation*; this arises from the fact, often observed in physiology, that, when sensory excitation becomes too violent, it diffuses itself all over the nervous system, and also to all the centrifugal paths, whether motor or inhibitory. Agitation, cries, palpitation of the heart, and generalized convulsions, are the effect of the penetration of the excitation into the first; while trembling, stupor, emotional flushing, and cardiac syncope are caused by its extension into the second. This principle is in some small degree opposed

to the preceding facts, which are rational, while it is an empirical one. At the same time it is observable that the attention demanded by the execution of irrational, useless and aimless actions distracts that which is involuntarily brought to bear on the pain, and thus acts as a soothing agent with regard to the latter (*duobus doloribus simul obortis, non in eodem loco, vehementior obscurat alterum*).

In spite of all the research of which it has been the subject, the mechanism of internal motor reactions of an emotional nature is still very obscure. As a set-off we have very exact information with regard to the muscular actions which imprint such a characteristic emotional significance on the features. This information we owe to Duchenne (of Boulogne). This author has discovered, in local electrization of the facial muscles, a very faithful analytical method of reproducing the expression of the principal emotions on the face of a subject who is not at the time under their influence.

3. **Emotional expressions of the human face.**—Emotion is shown on the face by the contraction of one or more muscles which, arising from a fixed insertion on the skull, displace certain portions of the skin, either hollowing it into wrinkles, or removing those already existing, thus changing the expression. Amongst these muscles are some which are by themselves completely expressive (frontalis, corrugator supercilia, zygomaticus major). Others are only *expressive in a complementary manner*, that is, are only adapted to complete or modify the expression produced by other muscles (palpebral portion of the orbicularis, transversalis nasi, platysma myoides). Lastly, there are yet others which are *little or not at all expressive*, either by themselves or in association with other muscles (buccinator). In the association of the facial muscles amongst themselves, the combinations are made up of but few elements (two, three, rarely four muscles). These contractions of the facial muscles, by themselves alone very expressive, may also be combined with gestures, bodily attitudes, and visible vascular and secretory modifications (paleness or flushing of the face, secretion of tears), all of which complete the expression.

Muscles of expression.—Physiological analysis has hardly investigated any except the *facial muscles*, which, after all, are the most essential element. The analysis consists in submitting these muscles, either singly or in twos and threes, to an artifical stimulus (electrical) directly applied to them. The muscle or muscular association thus brought into play shows the external expression (purely objective) of an emotion, of which the internal phenomena (subjective) are entirely wanting in the person experimented on. In order to avoid having to take into account reflex effects or painful manifestations which arise from the concomitant stimulation of the sensitive cutaneous nerves, Duchenne

operated on an individual suffering from a sensory facial paralysis, in such a way that the stimulus applied to the neuro-motor apparatus of the face acted only on this apparatus, to the exclusion of any other.

Attention to external objects.—This is characterized by an elevation of the eyebrow and the upper eyelid, while at the same time transverse folds are formed on the brow. This expression is caused by the *frontalis* muscle, whose insertion posteriorly permits an elevation of the eyebrow at the moment of its contraction. If exaggerated, this expression becomes one of *astonishment.*

Reflection.—Reflection is a state of the mind which causes the attention to be concentrated internally, to the exclusion of all external impressions; consequently it is a condition the reverse of the preceding one. Its mechanism is also the converse of that of the latter, and is executed by a muscle antagonistic to the frontalis muscle. Reflection is shown by a lowering of the eyebrow and an obliteration of its curve, while at the same time the lines on the forehead disappear.

This expression is caused by the contraction of the *superior half* of the *orbicularis palpebrarum muscle.*

Pain.—Both moral and physical pain is shown by a fold of the eyebrow, which is raised upwards and outwards by the contraction of the *corrugator supercilii.* This is an oblique muscle taking origin above on the frontal bone inserted below

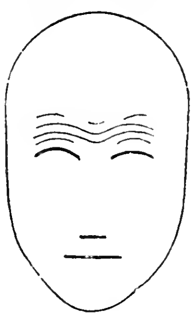


Fig. 162.—Attention.
Contraction of the frontalis muscles.

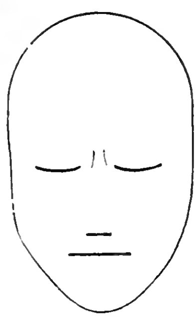


Fig. 163.—Reflection; meditation.
Contraction of the orbicularis palpebrarum.

in the middle of the eyebrow. Folds concentric to the inner curve of the eyebrow appear on the brow close to the root of the nose.

Menace.—This is shown by a lowering of the inner half of the eyebrow, and by transverse folds on the root of the nose, caused by the contraction of the *pyramidalis* muscle. This muscle is inserted below on the nasal bones, above on the deep surface of the skin of the inter-superciliary space.

Laughter.—In laughter the commissure of the lips is drawn upwards and outwards; the buccal opening is thus transversely enlarged, and ceases to be rectilinear. This displacement is due to the contraction of the *zygomaticus major* muscle. A very characteristic fold of the face, the naso-labial furrow, which ends in the commissure, becoming displaced by being drawn upward and outward, and at the same time ceasing to be rectilinear, forms a curve concentric with the commissure. The skin of the cheek becomes more prominent and forms radiating folds toward the external angle of the eye (crow's feet), and this augments the shadow below this angle, and almost gives rise to the belief that the eyelid has changed its place.

Weeping.—The expression of weeping is the exact opposite of that of laughter, so far as regards the direction impressed on the commissure and on the naso-labial furrow. The commissure is drawn downward; the furrow is displaced in the same direction, and the crow's feet have a tendency to be obliterated. These concomitant displacements are due to the contraction of the *levator labii superioris* and *zygomaticus minor* muscles. These muscles, more or less parallel to

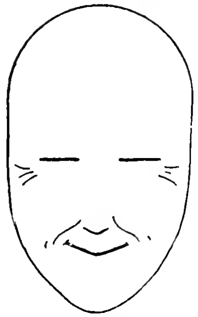


Fig. 164.—Laughter.

Contraction of the zygomaticus major muscle.

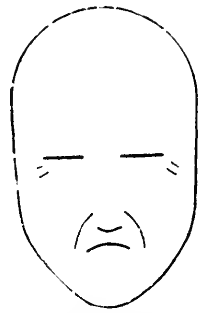


Fig. 165.—Weeping.

Contraction of the levator labii superioris.

the zygomaticus major, have, like it, a fixed insertion on the cheekbone or neighbouring bones (internal edge of the orbit) and, descending more or less obliquely, have their mobile insertion in the upper lip. But while the zygomaticus major, having the most external position, is attached near the commissure, the others are inserted in the middle part of the lip. From this arises the obliquity in an opposite direction which is communicated to its upper border by the contraction of one or other of these muscles. A third muscle, *the levator labii superioris*

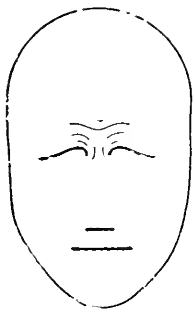


Fig. 166.—Grief.

Contraction of the corrugator supercilii muscle.

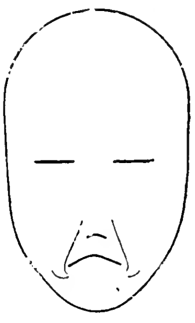


Fig. 167.—Discontent; scorn.

Contraction of the depressor anguli oris.

alæque nasi, is attached above to the internal border of the orbit and below to the wing of the nose and to the upper lip, near its median portion. This muscle increases the obliquity of the lip, at the same time dilating the wing of the nose. It raises *en masse* the internal part of the naso-labial furrow, hollowing it into a deep channel which is filled up by tears; this is the muscle of *violent weeping*.

Lubricity.—According to Duchenne, the expression of this feeling consists in the vertical folds of the lateral surface of the nose, which result from the contraction of *the compressor narium*. This is a digastric muscle, disposed in the

form of a girth over the bridge of the nose, and attached by its free extremities to the skin of the cheek and nose.

Disdain, scorn and *disgust* derive their expression from modifications of the position of the lips, especially of the lower lip. The expressions which result from the action of *pressing the lips together when displeased* or *of pouting*, are familiar to all of us. These expressions are due to the contraction of the *orbicularis oris of the mouth*. In the first case this contraction is limited to the internal fibres of the muscle, which press the buccal opening closely together in the same way as a purse is closed. In the second case the contraction is limited to the more eccentric fibres, whose isolated contraction causes the lips to project in the form of a funnel.

The *buccinator* muscle, important for mastication, articulation and for playing on wind instruments, takes no part in the expression of the emotions.

The *depressor anguli oris muscle* attached below to the lower jaw outside the symphysis, has its free insertion near the commissure of the lips. It consequently lowers this commissure, giving an obliquity to the buccal opening in the same direction as that caused by weeping; but in this case the obliquity is caused by the lowering of the commissure instead of the raising of the middle part of the upper lip. The naso-labial furrow is drawn down and becomes almost rectilinear. Slightly accentuated, this expression is that of *sadness*; more accentuated, it becomes that of *scorn*. The semi-occlusion of the eyelids caused by the contraction of the *orbicularis palpebrarum* (a special muscle of the eyelid) often accompanies and completes this last expression of the furrow.

The *depressor labii inferioris* has, like the preceding one, its lower insertion at the front part of the horizontal branch of the lower jaw; its fibres, which are oblique both above and inside, are inserted all along the lower lip. Contraction of this muscle, by projecting the lower lip, expresses disgust.

The *platysma myoides*, to a bundle of which the name of the *risorious of Santorini* has been given, is not by itself a muscle of expression; further, this muscle expresses neither mirth nor gaiety, but rather a *grin*, or a forced and menacing laughter.

3. Anatomical data

Definite relations exist between the cerebral cortex and the subjacent grey matter (which extends from the thalamus, the corpora-quadrigemina and the geniculate bodies as far as the grey axis of the spinal cord). These relations are effected by fibres which, from these masses of grey matter, extend to the cortex; conducting fibres, partly ascending and partly descending. The most accurate method of ascertaining these connexions is that of the degenerations of which the nerve fibres are the seat after the destruction of the cerebral cortex. This degeneration may be produced experimentally upon animals or may be occasionally met with in man as a consequence of diseases of the brain.

The degenerations which, arising from the destruction of the grey cortical matter, extend to its subjacent parts, are extremely numerous, as indeed are all those observed in these complicated regions of the nervous system. Amongst them may be found the three well known varieties (Wallerien, ascending and atrophic degeneration), distinguishable from each other by certain characters,

but especially by the order in which they appear. The Wallerien is the first to make its appearance, and is also the most marked; it attacks the fibres whose cells of origin have been either destroyed or separated from them (the pyramidal and analogous tracts).

Ascending degeneration, slower in its appearance than the former, progresses upward, little by little, to the cells whose terminal fibres have been cut or resected (for example, the fillet [or *ruban de Reil*] and the nuclei placed on its course). Although these two orders of degeneration are not in all cases absolutely easy to distinguish from each other, it is generally possible to make a division between the ascending elements (sensory) and the descending elements (motor) in the complicated tracts which unite the covering of the hemispheres to the subjacent nervous strata.

Atrophic degeneration is still slower in appearing, and is less allied to the destructive alterations which attack a region of the nervous system which is of any importance. Not only are the directly injured fibres altered in one or other direction (according to the portion removed), but in the end the nerve elements to which the foregoing communicate the impulse, ceasing to receive this latter in sufficient quantity or suitable quality, themselves undergo a certain degree of atrophy, as is indeed the case with all parts of the living body when condemned to functional immobility.

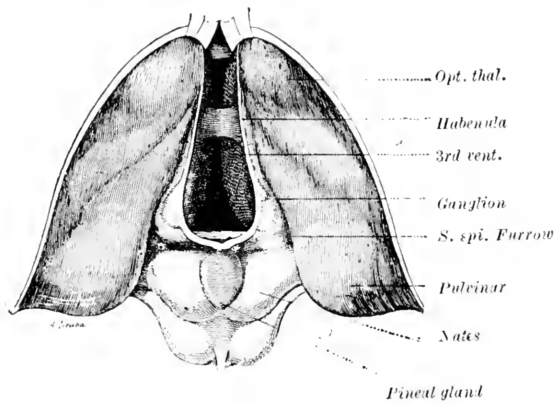


Fig. 168.—The optic thalamus, the corpora quadrigemina tubercles, the pineal gland, and the habenula.

The cerebral cortex and the optic thalamus.—The cortex of the brain may be divided into a certain number of regions, each of which answers to one of the senses. These regions are themselves capable of subdivision into areas or smaller spaces which correspond to distinct and localized functions (which are especially recognizable in the order of motor phenomena). *The territorial divisions of the cerebral cortex are anatomically and functionally repeated in the optic thalamus.* This is well shown by those secondary degenerations which invade this ganglion as a consequence of limited destructions of the surface of the hemispheres.

The optic thalamus is formed of a certain number of distinct nuclei which, according to their position, are described by the names of *ventral, anterior, lateral* and *median* or *internal.* To these must be added the pulvinar, the internal and external geniculate bodies, the mamillary body and the nucleus of Luys.

The anterior and internal nuclei radiate in the frontal lobe; the lateral nuclei in the parietal lobe; the ventral nuclei in the operculum; the posterior portions of the thalamus, that is to say the pulvinar, with the occipital lobe and also with the first and second parietal lobe; the internal geniculate body and the posterior nucleus with the temporal convolutions.

4. Functions of the optic thalamus

The functions of the optic thalamus were for a long time enveloped in the deepest obscurity. Vulpian acknowledged that our knowledge

on this point was entirely insufficient. Meynert, whose inductions are based especially on an anatomical foundation, regarded this ganglion as an important reflex centre; but this view was entirely wanting in precision.

A. Clinical facts.—It is to clinical observations that we owe the solution of this problem; they have shown us the distinction which exists between different kinds of motor paralysis due, on the one hand, to lesions of the optic thalamus, and on the other to alterations of the cerebral cortex. Experiments have also supplied data confirming this distinction.

1. **Superior and inferior facial.**—The facial muscles, to which are distributed the branches of the facial nerve, may be divided into two regions. The first, *superior*, known as the area of distribution of the superior facial nerve, comprehends the muscles which surround the orbital cavity (frontalis muscle, the orbicularis of the eyelids and the corrugator supercilii); the second, *inferior*, known as the area of the inferior facial nerve, comprising all the other muscles of the face. The terms *superior* and *inferior* are here used only to indicate the position of the muscles in the face.

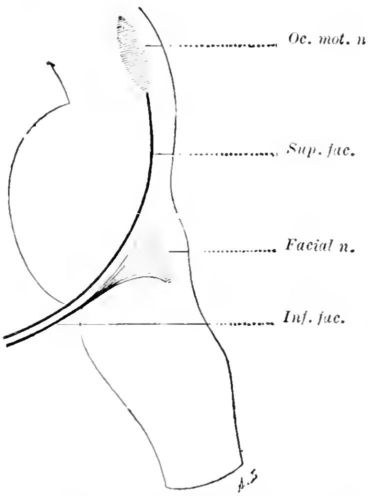


Fig. 169.—Superior and inferior facial (after Mendel).

The nucleus of the oculo-motor governs all the functions of ocular motricity, including the opening and shutting of the eyelids (this latter by the path of the superior facial).

If, on the other hand, the motor elements of any particular nerve are traced from the cortex to the muscles, it is found that they are formed (like all other motor elements of the same order) of at least two superposed neurons. One of these is a *deep neuron*, cortico-bulbar; the other is *peripheral*, bulbo-muscular.

2. **Deep and peripheral facial.**—When paralysis, of whatever nature, attacks the *peripheral* facial nerve (at its origin or during its intra-osseous course), it scarcely discriminates between its superior and inferior elements mixed in the same trunk. The paralysis is then called total, and this both because it affects all the fibres of all the facial muscles together, and also because it suppresses as regards these every source of excitation (voluntary, instinctive and reflex). It must then be considered as both complete and radical.

When paralysis attacks the *deep* facial (either in the cortex or its

intra-capsular course), it affects much more varied forms. This is due to the, anatomically speaking, very well marked separation between the superior and inferior facial which is here present, and also to the great variety of functions displayed by the elements composing the superior facial nerve. Its situation in the internal capsule is in the anterior portion of the "knee" of this structure.

In lesions of the deep facial (whether cortical or capsular) it seems, at first sight, as though only the inferior part of the peripheral facial were paralysed, the superior portion remaining immune. It is true that the features are drawn to one side and the corresponding cheek becomes loose and flabby (so-called inferior facial), while certain movements are preserved by the frontal muscles, and especially by the orbicularis (superior facial).

But, on examining the condition more closely, it will be found that the superior facial does not escape paralysis; it is merely that this paralysis is of a particular kind. In repose the palpebral opening appears slightly enlarged; this indicates a certain amount of *paresis* of the orbicularis (occasionally it is true, this opening is found narrower when the weakened muscle is, as sometimes happens, the seat of post-hemiplegic contractures). The folds of the brow are unequal as regards the two sides: this also indicates a paresis or a slight contracture, according to circumstances, of the frontalis muscle. Associated movements, such as blinking of the eyes, which may be reflex or involuntary, are still capable of performance, though more slowly on the side attacked by paresis. But dissociated movements, that is to say, the *isolated occlusion of one eye on the paralysed side, are impossible* (Pugliese and Milla).

3. **Paralysis of the voluntary function.**—To sum up, in these conditions paralysis has not caused the complete disappearance of either the reflex movements, the muscular tone, or even of those movements which become associated ones by being involved with voluntary movements; but it has suppressed certain localized movements which are *unilateral and acquired by education*, movements having, for this reason, in a high degree that *voluntary* character which is opposed to the reflex quality, and whose nervous mechanism appertains to certain differentiated areas of the cortex and of its subjacent fibres. In other words, *paralysis has in this case attacked the voluntary functions of the deep facial, allowing its reflex and emotional functions to remain unimpaired:* it is also possible for a lesion to attack the latter without molesting the former.

In hemiplegia it may be said, speaking generally, that the degree of paralysis of the muscles is the more marked in proportion to the

amount of asynergetic function possessed by them, that is to say, the more independent they are of associations and united action. As it is possible for these muscles to exercise different functions, one synergetic and the other asynergetic, it may also be said that the more independent the function under consideration, so much the more marked is the paralysis. Muscles may be paralysed as regards one function and continue active as concerns another.

The cortical region from which the superior facial nerve arises is situated in the inferior third of the ascending frontal convolution, opposite the base of the second frontal. Its area lies above those of the tongue and the mouth.

Independence of movements acquired by education.—The orbicular muscles have (at least in most people) acquired by education their independent and asynergetic motricity. In order to see better while performing certain actions, we have formed the habit of shutting one of the eyes, keeping the other open. It is the exception (apart from paralysis) to meet with subjects who are incapable of separately closing one of the eyes.

The frontal muscles only contract synergetically.

The corrugator supercilii muscles also only contract together. However, it is possible by study and practice to acquire the power of separately contracting each muscle of the face (Sikobsky).

The facial muscles are capable of performing *reflex* actions, *emotional* (instinctive) actions, and *voluntary* actions. These three kinds of actions bring into play the same muscles by means of the same nerve fibres in the peripheral facial (bulbo-muscular fibres). But, in the deep facial, these three orders of actions affect distinct and partially independent systems. This is demonstrable as regards at least some of these actions.

4. **Voluntary paralysis with preservation of the expression of the emotions.**—Certain patients suffering from hemiplegia are incapable of voluntarily impressing any movement on their paralysed face ; but if they are suddenly seized by a sad or gay emotion, these same muscles, though refractory to the will, give an expression of sadness or joy to the face (A. Magnus).

5. **Paralysis of the emotional expression with preservation of the voluntary movements.**—Conversely to what has just been said, some paralytic subjects retain the power of voluntarily contracting the muscles of the face and of moving the features ; but, should an emotion unexpectedly upset them, the face (perhaps one side only) is quite incapable of revealing it. It may be that at the same time the reflex or automatic movements of respiration are abolished (Ch.Bell, Stromeyer).

However, this dissociation is somewhat exceptional, and paralysis may simultaneously abolish the expression of the emotions and of the will; but when the dissociation exists it affords opportunity for an interesting analysis.

Different localizations of lesions in the two cases.—Paralyses of voluntary actions are due to lesions of the cortex or of the fibres of projection directly connected with it (cortical and subcortical lesions). If, when these lesions exist *the optic thalamus remains intact, the expression of the emotions is still possible.* The nuclei of the corpus striatum may be injured or even destroyed, and so also may the internal capsule, still the result is the same (Nothnagel).

B. Experimental facts.—According to Bechterew, the optic thalamus forms the chief centre or culminating point of a particular system, and is in a certain degree independent of the cortico-bulbar system with which it is, however, analogous, though very much more simple. Like the cortex, this system is attached to the medulla oblongata and to the spinal cord by fibres of projection, both sensory and motor, which are special to it.

This system is a reflex one: the impulses which ascend to it from the different senses are here reflected as motor acts. These acts, though automatic, are so in a complicated manner, and the sensation of which they are the expression is an emotion, an instinct.

The optic thalamus, then, would answer to a functional localization of this order; it is the principal locality for the elaboration of the emotions. Its connexions with the cortex are numerous; nevertheless, it may act independently. In animals, when the cerebral cortex has been removed while the optic thalamus is retained, stimulation of the organs of special sense provokes reflex movements of expression, which are liable to be mistaken for those of emotional expression such as arise in animals under sensorial excitation of the same nature. These stimuli cause grinding of the teeth, bristling of the fur or feathers, raising of the ears, etc., all signs of *pain* or *anger*. Painful stimulation of the skin will give to the features a *hostile* expression. On the contrary, if the skin of the back be caressed (in the cat), an agitation of the tail will result, and at the same time the purring, which in this animal is a sign of *pleasure*.

Not only stimulation of the external senses, but also of those which arise in the depths of the organism as a consequence of its general wants, have analogous effects; it is thus that the sensation of hunger excites, in the animal deprived of the cortex, movements which have a relationship with nutrition. The bird strikes the ground with its beak, and the guinea-pig opens its jaws widely. This instinctive move-

ment of the jaws is observable in cases of prolonged inanition (voluntary) (J. Soury).

1. **Motor tracts appertaining to the optic thalamus.**—These instinctive movements imply the existence of motor tracts belonging to the optic thalamus, and which connect it with the nuclei of motor nerves both bulbar and medullary. These paths, however, are still but little known anatomically. In any case, the cortico-bulbar tracts are here out of court, as these complicated movements are observable when the pyramidal tracts, in consequence of the removal of the cortex, are entirely degenerated.

The efferent fibres of the optic thalamus (thalamo-bulbar fibres) pass into the upper stratum (tegmentum) of the crus cerebri, while the pyramidal fibres enter its lower stratum (crusta). Hence it follows that it is possible for a sub-thalamic lesion of these fibres (in the pons) to paralyse emotional movement, just as a sub-cortical lesion of the pyramidal tracts may paralyse a voluntary movement (Huguenin). *The destruction of the optic thalamus in animals, as in man, allows the voluntary movements to persist, but entirely suppresses all movements of an emotional nature* (movements of the face, ears, and, in animals, of the tail).

2. **Functional relationship between the cortex and the optic thalamus.**—The functional distinction which is apparent between the cerebral cortex and the optic thalamus does not imply an absolute independence between the first and second of these two systems. The anatomical connexions existing between them are numerous. It is obvious that impulses are transmitted from one to the other, and reciprocally. When both are intact and their connexions maintained, the chain of psychical acts becomes longer and the complications so much the greater. The emotions may have their starting-point either directly in the external stimuli, which reach the organs of the senses (as in the animal whose cerebral cortex has been removed), or in the same stimuli, but by the intermediation of the *ideas* and the *memories* which they have awakened, or left, in the cortical systems. Emotion may be brought into being suddenly as the result of remembrance, that is to say, without any apparent immediate provocation, but in reality arising from an anterior incitement preserved in a latent state in the brain.

Inhibitory action of the cortex on the optic thalamus.—The optic thalamus not only receives impulses (motor) from the cortex, but it also experiences from it an inhibitory influence, which, when the emotion is not too strong, prevents the external manifestations of the latter. In hemiplegic patients who, having lost the power of voluntarily moving the facial muscles, have yet preserved their emotional motricity, laughter or tears may often be observed to burst forth without any appreciable cause, or on the most trivial grounds. This is an indication

that the inhibitory powers which have their seat in the cortex are enfeebled, or have disappeared (Oppenheim). This debility is naturally more pronounced in the case of bi-lateral lesion of the cortex, and it is then, especially, that *spasmodic laughter and tears* are observed.

With regard to the mechanism and the precise seat of this inhibition, it must be admitted that they are far from being known. Many hypotheses may be formulated on this subject. This inhibitory function might be brought into action by means of fibres going from the cortex to the optic thalamus itself. Some, like Oppenheim, infer the existence of cortico-bulbar inhibitory fibres which restrain the motor action of the nuclei seated in the pons and in the bulb. Any lesions in these conducting fibres would leave the field open to tempestuous and disordered manifestations of the emotions. Brissaud maintains the exist-

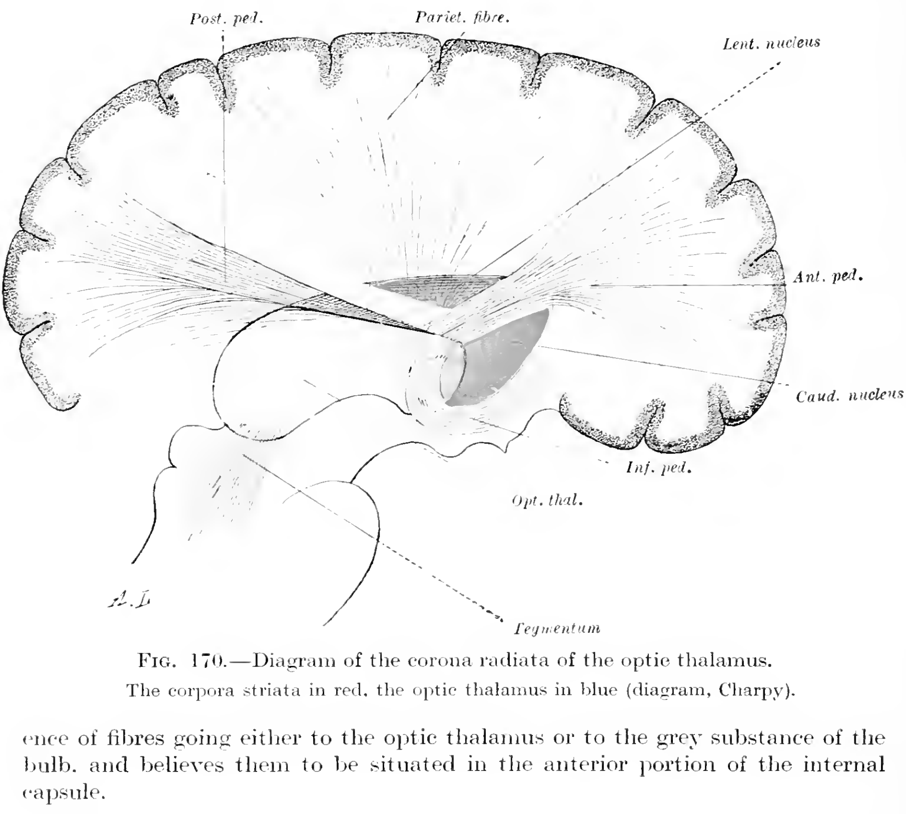


FIG. 170.—Diagram of the corona radiata of the optic thalamus.
The corpora striata in red, the optic thalamus in blue (diagram, Charpy).

ence of fibres going either to the optic thalamus or to the grey substance of the bulb, and believes them to be situated in the anterior portion of the internal capsule.

3. **Emotional reactions of the deep organs.**—Emotion is revealed not only by movements of the face, but also by changes in the movements of the respiration, by disturbances of the cutaneous circulation and of the secretion of the lachyrmal gland, and, in fact, of all the functions of vegetative life which are dependent on the great sympathetic. The optic thalamus controls these different functions. Stimulation brought to bear on the grey commissure of the thalamus causes *secretion of tears, dilatation of the pupil and exophthalmos.* The optic

thalamus also acts on the *movements of the heart, the stomach, the intestines and the bladder.*

The optic thalamus, to which may be added a certain portion of the lenticular and caudate nuclei, may be decomposed into a series of distinct centres, whose stimulation induces those modifications of the internal functions which are observable in the display of the emotions

Christiani has influenced the movements of respiration by stimulating the floor of the third ventricle. Bechterew and Mislawsky have noticed vaso-constriction and elevation of pressure to follow stimulation of the *globus pallidus* and the optic thalamus. The same authors have observed the effect of stimulation of the different segments of this ganglion on the movements of the small intestine (strengthening by the excitation of the middle region, weakening by that of the external region). The stimulation of the antero-external region increases the contractions of the large intestine and causes defecation. That of the inferior internal region near to the grey commissure causes tears to be secreted. That of the inferior part of the anterior nucleus causes the bladder to contract.

5. Functions of the corpus striatum

The corpus striatum, amongst all the nervous organs, remains the one whose functions are the most obscure.

Comparative anatomy displays this ganglionic mass in a ratio of development inverse to that of the cortex of the brain. In osseous fishes this latter is represented only by a thin layer of epithelial cells, forming the roof of the ventricle of the anterior brain, which is equivalent to the two lateral ventricles of the brain of mammals. That is to say, in these animals the cortex of the hemispheres does not exist, or exists only as a mass of grey matter, the cells which enter into its constitution being ependymal elements like those which line the nerve cavities.

Morphological equivalency of the parts.—The anterior lobes of the brain in osseous fish are then equivalent to the ganglia of the base (opto-striate bodies) of mammals (Rabl-Ruckhard). A transverse, or interlobar, commissure connects them. A basal bundle, or kind of peduncle, is detached from them, which is formed of fibres, the first ascending (sensory) the second descending (motor). The axis-cylinder prolongations of the first-named form arborizations which come into direct contact with the dendrites of the second, without any interposition of short neurons of association ; or, at any rate, these elements are few in number and not very obvious (Van Gehuchten). The commissure is formed by a decussation of a portion of the sensory fibres, of which some reach the opposite lobe, while others remain in the corresponding lobe. This commissure is in no sense the equivalent of the corpus callosum, seeing that the hemispheres are wanting.

Functional non-equivalence.—As it is impossible to deny that such animals

possess, not merely the faculties of instinct, but even a rudimentary intelligence, we may conclude from this that these faculties may be exercised by nervous organs other than the brain properly so called, organs which display a rough sketch of it.

The basal bundle, which is easier to distinguish in batrachia, manifestly goes from the corpus striatum to the spinal cord (strio-spinal tract, equivalent to the motor pyramidal tract), while fibres ascend from the spine, the bulb and the pons to the corpus striatum (equivalent to the sensory tract). The first descend in the anterior columns of the spinal cord, and the second may be followed into the antero-lateral columns (Van Gehuchten). In these animals (batrachia) a rudiment of the corpus callosum, and a rudiment of the cortex are sometimes observable by the appearance of a few cells in the epithelial membrane which covers the ganglia of the base. Fibres of association between the corpus striatum and the thalamus, which are well marked in batrachia, may also be observed.

Reptiles, birds : development of the cortex.—In reptiles an elementary sketch of the cortex is observable. In birds the sketch is carried farther ; but still only exists as a thinnish membrane. Still it is possible to distinguish in this rudimentary cortex five superposed layers, namely : the molecular zone, a layer of small stellate cells, a layer of large stellate cells and of large pyramidal cells (that is to say, cells of association and cells of projection), a layer of deep stellate cells, and finally an epithelial zone.

An important detail is that these cells of projection which start from the third layer of the cortex, and are, so far, few in number, are not substituted for those of the corpus striatum, but merely added to them. The corpus striatum preserves its basal bundle, this latter retaining its relations with the spinal cord.

Progressive building up ; displacement of the directive functions.—Thus the study of comparative anatomy enables us to comprehend the progressive building up of the nervous system. We see how it establishes and completes each of the superposed layers before beginning the construction of the next layer, primary ganglia, spinal cord, basal ganglion and cortex. At the same time this superposition, although it may not cause the disappearance of anything which has already been built up, does not proceed without a certain fluctuation between these successive formations ; the last comers seizing upon and developing a part of the functions assumed by the primitive nervous organs when existing alone. The spinal cord and the basal ganglia lose their relative importance in proportion to the advances made by the brain towards the preponderating position it acquires in the human race.

Directive sense, not identical in all species.—From another point of view the brain itself, which owes its high functions to the development of specific aptitudes, has not, in its evolution, always directed these aptitudes in the same manner in all animals. Thus the psychical functions of one may differ from those of another, not only in quantity, so to speak, but also in quality. Our ideas proceed from our sensations ; but they proceed unequally, because our different senses have not an equal value, and therefore take a very unequal share in the formation of ideas. The same thing occurs in the animal world ; only in comparing them together it will be found that certain senses, very predominant in the one, may be much weakened or almost annihilated in the other. From this we are forced to a somewhat unexpected conclusion, namely, that representations of the external world assume different forms in each case, according to the specific nature of the sensations which are the original elements of these representations.

Sense of smell in reptiles ; vision in birds.—In this respect the comparison of birds and reptiles is very significant. In the latter the olfactory sense has a preponderating development and is found, unlike the rest of the senses, to be connected with the rudimentary cortex appearing in their brain. In the first

case (that of birds) it is the sense of sight which directs the reflected acts of the animal, and this substitution is obviously necessary in beings which, by soaring in the air, have in a certain measure changed their medium. Further, in birds, between the basal optic ganglia and the cerebral cortex a very important tract will be found. This tract is wanting in reptiles, and in them the principal connexion of the brain with the superior centres is effected by means of highly developed olfactory radiations.

Physical and psychical elaboration.—A sense is an assemblage of highly complicated functions, in which numerous actions are concerned. These actions, by a continuous gradation, extend from the purely physical phenomena in which they have their origin, to the psychical phenomena by which they are characterized. The nervous paths in which each of these acts is successively displayed respectively secure the performance of these acts. It follows from this that the state of perfection of a sense may be considered from very different points of view, according to which of these actions is in question, and especially as to whether it is their force and physical precision or their psychical value which is under consideration. The sense of sight in a bird is more piercing than it is in a man; this is due to the fact that, not only the globe of the eye, but also the whole nervous assemblage which attaches it to the sub-cortical ganglia, is, in the first-named, more developed than in the second. But man, from his comparatively imperfect visual sensations, derives ideas and representations which are absent in the bird, because in the cerebral cortex he has at his disposal a mechanism of transformation whose power is infinite in comparison with that possessed by the latter.

In the bird especially, a system of fibres is found, which from the sub-cortical ganglia returns to the retina by a centrifugal path, and which, though existing in man and other vertebrate animals, is in them much less highly developed (Perlia). The function of these fibres which, although centrifugal in their nature, lead back the nervous impulse to the sensory organs whence it arose, is still very obscure. The fact that the development of these fibres is proportional to the development and the perfection of the sense to which they belong is a proof that the part they here play is an essential one, though but little is known about it. It may be that they have some relation to the persistence of luminous impressions after their directly exciting effect has ceased; or perhaps to the preservation of these impressions in the memory and the power of re-invoking them.

Relations of the corpus striatum with the anterior portion of the brain.—Embryology describes the corpus striatum as an appendage of the fore brain. Comparative anatomy displays it to us exercising the functions (very rudimentary ones it must be owned) of the brain in beings (fish) in which the cortical covering is still absent. In superior mammals the method of degeneration proves the existence of *connexions between the cortex of the frontal lobe and the nuclei of the corpus striatum*, principally the caudate nucleus. A cortico-striate path exists, formed of fibres united in small bundles, which, following the course of the internal capsule, detach themselves from its anterior segment. These fibres penetrate, by preference, into the nucleus last spoken of (caudate nucleus), either by traversing it after giving collaterals to it, or by distributing themselves and coming to a termination therein (Marinesco).

Analogous fibres connect the cortex with the optic thalamus, and the corpus striatum is itself united to the thalamus. Lastly, these nuclei are themselves attached by connecting fibres to the nuclei of the grey matter of the pons.

All these paths are made up of elements of which some ascend and others descend; these elements convey the impulse in one or the other direction.

1. Experimental data.—As concerns the total function appertaining to such a system of co-ordinated elements, and more especially to the

corpus striatum, physiology has unfortunately up to the present time remained but ill-furnished with positive information.

Destruction.—Magendie advanced the theory that, after the removal of the two corpora striata, the animal showed an irresistible tendency to go forward. If this be so the corpus striatum would possess functions which are related to the movements of locomotion and of walking. The more recent experiments of Nothnagel and of Fr. Rezek have led these authors to the same conclusion. By destroying (with an injection of chromic acid by the aid of the syringe of Pravaz) a limited portion of the caudate nucleus, the first of these authors, and also Magendie, succeeded in producing circus movements, or those of progression in a forward direction in rabbits. Nothnagel calls the area of the caudate nucleus which is connected with these movements *nodus cursorius*. According to Rezek, a relationship of the same nature exists between locomotion and the *putamen* of the lenticular nucleus. It is impossible to say what share is taken in a lesion of this kind by the destruction, properly so called, and the stimulus which is the result of it; or, again, what part is played by the motor or inhibitory elements which are themselves destroyed or stimulated.

2. Supposed function.—These grey masses of the corpus striatum contain within themselves associations of sensory and motor elements, which transmit the impulse in the desired manner so as to secure the performance by the limbs of the movements by means of which progression is effected; and, it may be added, its continuance when once commenced. These movements are *automatic;* or, to put it differently, *involuntary*. They are produced by the arrival in the system which is adapted to their performance of an impulse which initiates them. They cease when another impulse arrests the preceding one and brings the automatic system back to a state of repose; they continue during the interval between these two impulsions. The initiation (or its cessation) is alone *voluntary*, and therefore the impulse which produces it comes from the cortex, or must have passed through it.

It must not be forgotten that the spinal cord contains associations which obviously effect co-ordinated movements. By itself it can cause the performance of only the simplest of these, such as swimming in the duck, but not walking, which demands the maintenance of an equilibrium, itself alone representing a complex function.

Stimulation.—François-Franck and Pitres have not observed any motor effect to result from the direct stimulation of the corpus striatum; neither has Carville or Duret noticed any effect of this nature. Nevertheless, by stimulating the internal capsule of a dog from which the

cortical centre of the anterior limb had been previously removed, and of which the corresponding fibres of the corona radiata were inexcitable, movements were provoked in this limb, no doubt through the stimulation of the healthy fibres coming from the corpus striatum. These same authors, after having successfully removed the corpus striatum, observed a marked weakness of the opposite side and a special circus movement (probably due to a lesion of the crura cerebri). If the extirpation is incomplete, contractures of the side opposite to that operated on are observable. These effects when summed up bear witness to the existence of a motor function.

Lépine has seen pseudo-bulbar paralysis to be produced by a lesion of the *putamen* (labio-glosso-laryngeal paralysis).

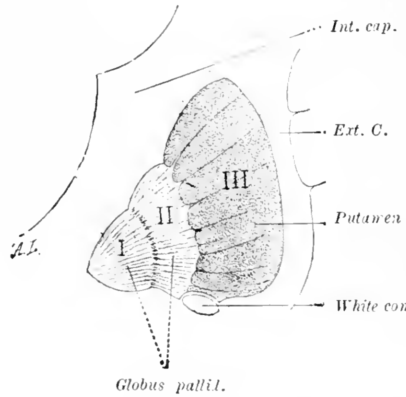


FIG. 171.—The three portions of the lenticular nucleus of the corpus striatum.

Frontal section, left side (after Charpy).

NUCLEUS OF LUYS: CORPORA QUADRIGEMINA; CORPORA MAMMILLARIA.—In the neighbourhood of the optic thalamus are other analogous formations which, like it, and indeed often with its assistance, are capable of co-ordinating into motor actions the impressions which come from the periphery, thus taking part in emotional and instinctive acts. As these grey masses are more particularly connected with the exercise of the special senses (sight, hearing and smell), their functions will be studied with regard to specific innervations. The sketch that we are tracing here of the progress of the impulses in the nervous system, and the functional modalities resulting therefrom, is made by taking as a guide principally tactile sensibility and the motricity of the skeleton.

6. Instinct in man and animals

Man possesses reason and animals instinct. These two forms of psychism sometimes resemble each other in a surprising manner, though fundamental differences at the same time exist between them. The resemblance is made more marked by the complexity and perfection shown in the workings of instinct. It is also shown by the certainty of this working, which is conducted through a series of operations from a given starting-point towards an end of a useful nature, which is steadily and inflexibly kept in view until attained. Instinct not only

directs the individual life of animals, but in a number of them also results in the formation of social organizations, in some way analogous to societies of human beings. Certain invertebrata, like bees and ants, are remarkable from this point of view.

Man, witnessing these acts, willingly acknowledges their similarity to those by which his own intelligence is manifested. The likeness in the effect produced induces him to admit a resemblance between the psychical processes which are in operation; this resemblance, however, is merely a superficial one. It is only necessary to place before the animal difficulties easily overcome by human intelligence to mark the difference which exists between reason and instinct.

Characters of instinct.—The instinctive act, like the intelligent act, has its starting point either in an excitation or a need (*instinctus*, pricking, *stimulus*), and resembles it also in having a determinate end for its aim. But in the animal this aim is an unknown one: *instinct is blind*. Intelligence, on the contrary, is conscious of the end it has in view, and indeed forms an ideal representation of it.

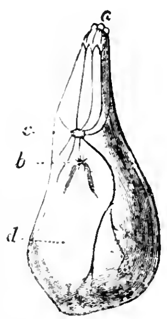


FIG. 172.—Nervous system of an ascidian (after Carpenter).

a, mouth; *b*, orifice; *c*, ganglion; *d*, muscular bag.

Fatality.—The operations of instinct follow each other in a rigorous order; the one gives rise to the other without contradiction, inversion or complication, and all follow a lineal series. They are the realization of an experiment, always the same one, the internal and intra-nervous determinism of which is rigid and inflexible. Instinct has only one solution when facing the problem placed before it; intelligence finds a great number. This results from the fact that, in the human brain, particular antecedent experiences have been subjected to a methodical classification. A crowd of possible acts have a parallel existence alongside the realized act, either resembling it more or less, or else differing from it. Intelligence knows the meaning of hesitation and doubt, instinct ignores them.

Innateness, heredity.—*Instinct is innate*, its operations make their first appearance at birth without imitation or preliminary education. That is to say, with Lamarck and Darwin, *instinct is hereditary*. Anterior experiences, brought into action by the animal from its birth, are not really its own, but those of its ancestors. The intra-nervous determinism which ensures their immediate realization is transmitted from them to it, by the same route and the same unknown means as those which secure the development of its organs, and the performance of the functions by means of which it reproduces a being resembling them in everything. Further, it may be said that *instinct belongs to the species*, either regarded as the aggregate of the beings forming it at a given moment, or as the series of those to be engendered in course of time. Intelligence, on the contrary, is capable of acquisitions, growth, and individual development. The inequality and the variety of its powers marks the personality of the human individual; the animal, however, is no more than a numerical unit in its species.

Relations with intelligence.—In nature there are no phenomena so opposed to each other that it is not possible to find for them a common basis. Between intelligence and instinct the difference is very striking, but at the same time their relationship must be acknowledged. In the animal, as in man, instinct and

intelligence co-exist in extremely unequal, but still recognizable, degrees. The operations of both are susceptible, not only of being mixed together, but also of being reciprocally transformed. In man instinctive acts become rational ones by progression, and acts of reason become instinctive by retrogression; the second of these transformations may be advantageous quite as well as the first. In the directive part that it assumes in us, intelligence, in proportion as in the course of development it reaches more elevated spheres, entrusts to instinct the performance of those inferior acts which have acquired their full perfection. In the animal, the opposite is the ease: while instinct directs the series of its acts towards an unknown aim, intelligence intervenes in the individual realization of each of them. The succession alone is traced in advance, while the details of the operations often contain much that is unexpected.

Psychical automatism.—Finally, intelligence and instinct resemble each other in the complexity of their actions; they differ in the *plasticity* of the first compared with the *rigidity* of the second. The plasticity of the intellectual processes is, of all their attributes and characters, the one that removes them furthest from physical or mechanical phenomena; on the contrary, the rigidity of instinct is a characteristic which approximates it to these phenomena. With the Cartesian school, this likeness has been pushed as far as an identification: for an extreme Cartesian an animal is an automaton, in the mechanical sense of the word. Although this opinion no longer possesses any adherents, the expression is preserved, but it does not now bear the signification of a pure mechanism.

Automatism is not incompatible with psychism of a determinate nature: individually conscious acts may succeed each other, and be linked together in a strict manner (with or without traces of memory), in the same way as purely mechanical acts. *Psychical automatism* is as comprehensible and as real as physical automatism. An automatism of this kind takes part not only in instinct, but in the intellectual processes themselves.

Comparative psychology.—When instinct and intelligence are studied in the animal series, it will be seen that they undergo a progression which, if not regular and continuous, is at all events marked, in proportion to the general development of this series. Instinct proceeds from a more elementary nervous manifestation, namely, the reflex, of which it is an elaborated form. It is impossible to deny the existence of links connecting intelligence and instinct, in spite of the dissimilarities and contradictions which these two psychical modalities present. In a similar way the comparative study of the nervous systems is instructive. Reflex action is carried out by a very simple system of ganglionic aspect, resembling that of the ascidians. The ganglionic chain of the invertebrata and the spinal cord of the vertebrata (both considered separately) represent types of this system which are already elaborated. Such a system is formed essentially by the association of primary neurons; that is to say, neurons proceeding directly from the integument to the ganglion (sensory neurons), and from the ganglion to the muscles (motor neurons), the ganglion itself being merely the link of association between them (with or without short neurons reinforcing and complicating this association).

Instinct is presided over by superstructures formed of secondary neurons, which are not directly connected with the integument as with the muscles. These superstructures proceed, by development and progressive extension, from the short neurons of association which already exist in the ganglia and the segments of the spinal cord. They form the origin of the brain. The supra-œsophageal ganglia of the invertebrate chain have this signification. Their development is in relation to that of instinct. This fact is more particularly demonstrated when a comparison is made between the nervous systems of animals (insects) of the same species, but which, by being organized into societies, are differentiated for

special social functions. Such are the ants, amongst which the workers, a queen, and the males are distinguishable. Instinct progressively decreases from the first-named to the last. The elaboration of the nervous system, however, still continues in the sense that, while the brain steadily diminishes from the workers to the males, in these latter the organs of sense and the primary neurons are more developed (Forel).

The vertebrata furnish us with a new field in which, as we have seen above, this comparison may be pursued.

C. INTELLIGENCE—THE BRAIN

Man occupies a place by himself in the animal world. His physical weakness forms a contrast to the potency of the means he has been able to create for himself. He has undertaken the conquest of the three realms of nature, and endeavours from day to day to bring them more and more into subjection to himself. Limited to an imperceptible space and a momentary duration in time, he extends his actions over great distances, reviews the past and operates on the future, thus preparing it in advance. This power is the gift of his intelligence, which reveals it in visible and durable works. It may also be added that the limits of this power are nowhere more observable than in the efforts made by it to analyse the springs of its own origin, and to penetrate the secret of them. Like sensation, whence it is derived, intelligence is inseparably connected with organization. This organization is that of the nervous system, and in it certain systems have been chosen and developed in preference to others. The sensory and motor functions of a mammal differ but little from those of man. Every organ of the special senses—smell, sight, hearing—may be more developed and more perfect in certain kinds of animals than in ourselves, and their strength and motor agility may be very superior to ours. But the senses are only instruments in the service of intelligence. The factors of intelligence do not lie in the senses themselves or in the inferior system which represents them, but in an assemblage of superior systems controlling the former.

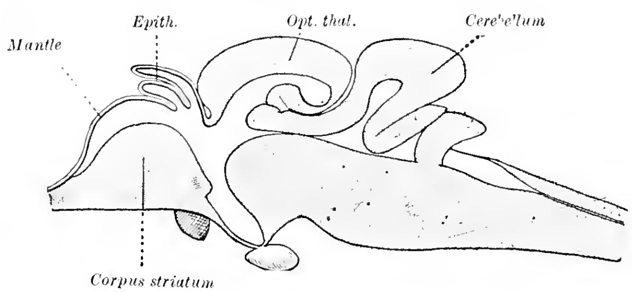


FIG. 173.—Brain of osseous fish (after Edinger). The mantle is reduced to an ephithelial layer.

Absolute and relative development.—If, like the organs of sense, we compare the spinal cordof man with that of mammals, we shall not

find this organ more developed in the former, but rather, on the contrary, deprived of certain functions which it has little by little yielded up to the brain. This last organ has, on the contrary, taken on a development striking even to the least instructed eye.

In the animal world the development of the brain is, in a certain way, connected with that of the intelligence. Those animals which most nearly resemble man are provided with a brain which, by its dimensions, its general configuration and its principal divisions, recalls the human brain (primates). In other mammals this type is modified; the structure tends to become simpler (carnivora). This simplification is very significantly expressed by the disappearance of the furrows which bound the convolutions: the brain from being *gyrencephalic* becomes *lissencephalic*. This degradation is the result, not of an uniform reduction of the different portions of the brain, but, on the contrary, of the unequal development, or the absence of certain of these parts. Or, as may perhaps be preferable, to consider the matter from the opposite point of view, the evolution of the nervous system is effected by adding and superposing, little by little, new systems to those already existing, and which are not susceptible of further improvement. These new systems give a new value to the organization, by augmenting the cohesion of the old systems at the same time that they displace the primitive tie which bound them together. In the amphioxus the brain is scarcely indicated, and the spinal cord fulfils the function of a directive centre. In certain fishes the basal ganglia are highly developed, but the cortex of the hemispheres is still wanting and is only represented by a non-differentiated epithelial ectodermic layer. In reptiles this cortex begins to be sketched in. In birds and mammals its development continuously progresses, and it tends more and more to usurp the functions of the subjacent centres.

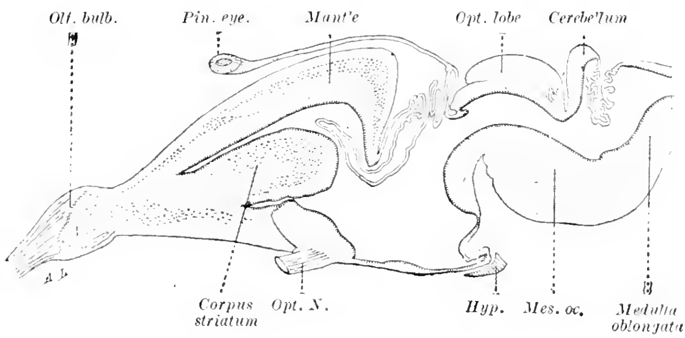


FIG. 174.—Brain of the reptile.
The mantle appears as nerve matter.

Difficulty of quantitative estimations.—This functional value, at once both

unequal and variable, of the superposed layers of the nervous system renders an estimation of the connexion existing between its development and the elaboration of these functions themselves extremely difficult to effect. No one function is enclosed in a circumscribed segment of the organism or of the nervous system; all are in a condition of mutual dependence. The localizations of them that we can trace only correspond to the characteristic modalities of these functions, but do not include them in their totality. The spinal cord is endowed with a sensori-motor function, which is a rough sketch of intelligence. The intellectual function of the brain does not debar this organ from possessing a senso-motricity, which here is not necessarily dependent on its highest psychical manifestations. Any anatomical limit between the two orders of functions is purely arbitrary, difficult to realize, and impossible to trace.

It may also be said that animals differ, not only in the degree of their intelligence, but also in the apparatus by the aid of which they maintain, and also manifest, that intelligence. These mechanisms are those of the senses and of the motor organs depending on them. In animal evolution the senses assume an unequal importance, substituting and replacing each other mutually, but without being equivalent to each other. A sense of an inferior order, like the sense of smell, having been the first attached to the rudimentary brain, is, owing to this act, found at the very foundation of instincts and intelligence. Superior senses,

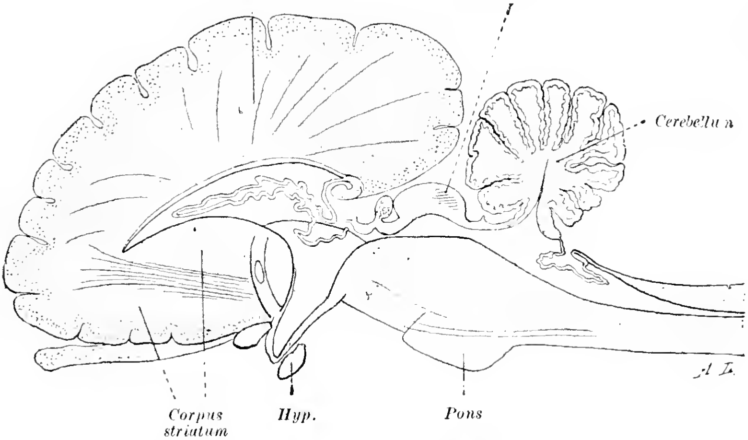


FIG. 175.—Brain of mammal (after Edinger).
Predominating development of the mantle.

like sight and hearing, are, on the contrary, connected with greater intellectual development. In animals of a similar organization, the sense of smell may be found persisting in some, while in others it has become atrophied (osmatic, anosmatic).

Thus it is obvious that a great number of circumstances help to complicate the problem, and to falsify the results of deductions which it has been attempted to draw in this direction. The development of the nervous system, whether estimated by its increase in weight, in volume, or in the superficies of its principal segments, depends on the *repetition of similar parts, as well as on the addition of new ones.* It is evident that the first of these two factors has no value as regards the development of instincts and of intelligence; and hence another difficulty arises, as it is necessary to consider what share falls to it, and then to deduct

that share from the numbers to be compared. All these causes of error dispense with the necessity of our entering into a more lengthy examination of the results.

1. Anatomical data: structure and connexions

We will now give a summary review of the organization of the brain and of its connexions with inferior systems. We will then set forth the results of the experiments by means of which efforts have been made to distinguish its proper functions, by comparing them with those of the other large segments of the nervous system. Afterwards we shall enter into the analytical study of these functions themselves, or, to put it otherwise, into that of the functional localizations attributable to the different regions of the cerebral cortex and its white matter. On account of its importance and the numerous observations and experiments with regard to detail which it permits, this study will be renewed in the second section on the *Systematic Functions*, in which specific innervations are considered.

The grey matter of the nervous system may, in the first instance, be divided into two portions or two essential groups. One is the grey bulbo-medullary axis prolonged, outside the vertebral column, by the ganglia of the great sympathetic and, in the skull, by the optic thalamus and a portion of the other ganglia of the base of the brain. The other is the cortex of the brain, to which a part of the corpus striatum is attached. Fibres of projection unite the first to the periphery by a double sensory and motor tract; other fibres of projection enable the two grey structures to form junctions amongst themselves by means of conducting fibres which ensure a transmission in the two directions. The different stages or portions of the first system are bound together by fibres of association. The different areas of the second are also united by fibres of the same description, which here assume an exceptional multiplicity and importance. The passage of these two kinds of fibres, or their decussation from one side of the body to the other, forms what are known in the two systems as the commissural fibres.

A. Cortex.—The layer of grey matter which covers the brain is described by the name of *cortex, pallium, mantle.* This superficial layer is folded on itself in order to form the anfractuosities and convolutions of the brain, with the obvious aim of increasing its extent in relation to the bundles of white matter which encroach upon it in different directions. It entirely covers the two hemispheres, except in the locality where they are penetrated by the crura cerebri, which unite them to the grey medullary axis, and by the corpus callosum, which connects the one with the other.

When cut, the cortex displays a series of stratifications, visible to the

naked eye or with the lens, and especially by transmitted light (Baillarger). Its histological study proves it to be composed of cellular elements, including several definite types analogous, if not similar, to those met with in the spinal cord, but in greater variety.

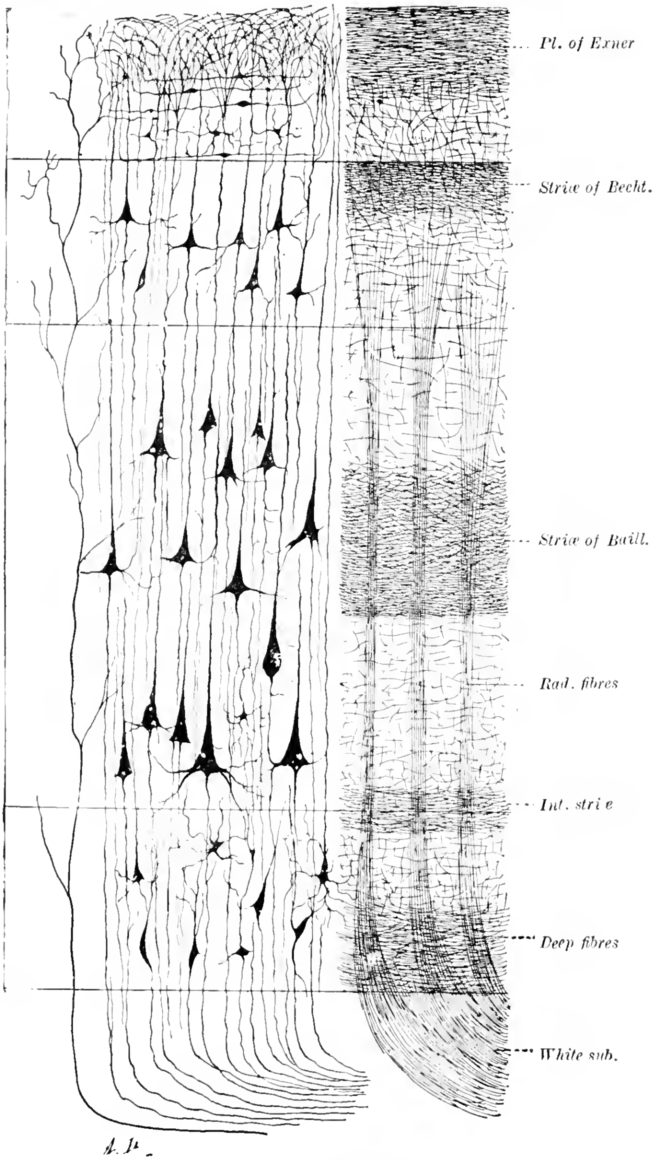


Fig. 176.—Cerebral cortex.

Diagrammatic section. On the left, the cellular layers; on the right, systems of fibres.—On the extreme left a sensory fibre is seen ascending.—1, 2, 3, 4, the four layers of cells; 2 and 3 representing pyramidal cells of differing size.

Histologists have observed that the structure of the cortex itself

corresponds to a kind of average type, which may be found throughout its extent. This type undergoes certain modifications, according to the localities, some elements predominating in number or in size in certain regions, in others effacing themselves, and reciprocally.

Structure.—The superposed layers of the grey cortical matter may be reduced to three, namely :—

(1) *The so-called molecular layer.*—This is composed of polygonal, fusiform, and triangular cells. The fusiform cells are the most characteristic of this layer : they are spread out in the direction of the surface of the brain and their prolongations, both protoplasmic and those of the axis cylinder, are limited to this layer itself and generally ascend towards the surface of the cortex. The others are not essentially different.

(2) *The layer of pyramidal cells.*—This layer is double as concerns some portions, triple as regards others : this is explained by the fact that the cells are increased in size in proportion to the depth to which they penetrate (small, medium, and large pyramidal cells), without any abrupt transition.

The pyramidal cell, if not the most characteristic element, is at any rate the one most easily recognized in the cortex of the brain. The base of the pyramid is turned towards the white matter ; its apex is lengthened above by a *principal prolongation* (protoplasmic or dendritic) up to the molecular layer : there it spreads out into a thick plume, bristling with short points having enlarged terminations. From the trunk of this principal prolongation shorter *collateral prolongations* are detached, these going off from the trunk at a right or acute angle. Lastly, at its base the cell always gives origin to *basal prolongations*, which are directed laterally or obliquely downwards. All these prolongations represent the polar field by means of which the cell collects the impulses.

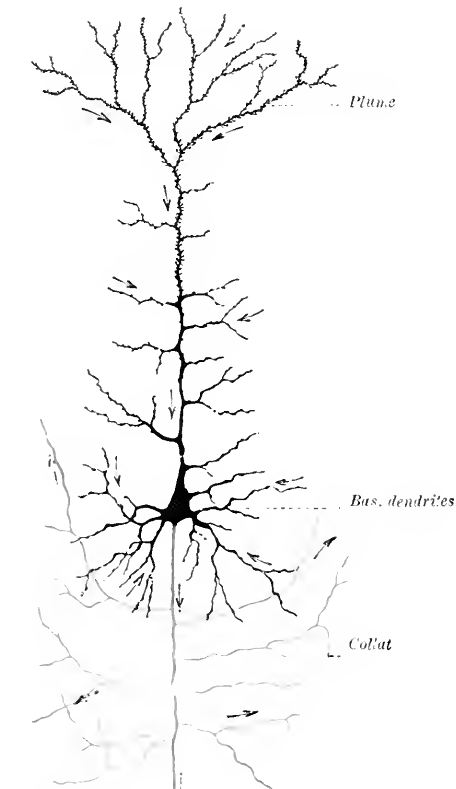


FIG. 177.—Pyramidal cell of the cortex.

Its dendrites in black : its axis cylinders and its collaterals in red.

The axis-cylinder prolongation arises from the base of the cell (rarely from one of the prolongations), it plunges into and disappears in the white matter of the *centrum ovale*. Before leaving the cortex, it gives off some collaterals, which are there exhausted. The axis-cylinder prolongation, however, descends and sometimes reaches very remote localities, for example : the grey matter of the medulla oblongata or of the spinal cord. From what experimental study

and the degeneration of these nerves teach us, they may be described as descending or, in other words, motor in function.

It must be observed that, between these cells, others furnished with a short axis cylinder exist, these representing what are usually called elements of association.

(3) *The layer of polymorphous cells.*—This layer, regarded as being double by Meynert, who divided it into irregular cells and fusiform cells, is described as a single one by Cajal, who has given it its new name. The cells are ovoid, fusiform, stellate and triangular ; in spite of their irregularity, they still have some resemblance to the preceding ones. Their protoplasmic prolongations never ascend up to the molecular layer, and their axis cylinder is a descending one.

This layer also encloses somewhat characteristic cells, called those of Martinotti,

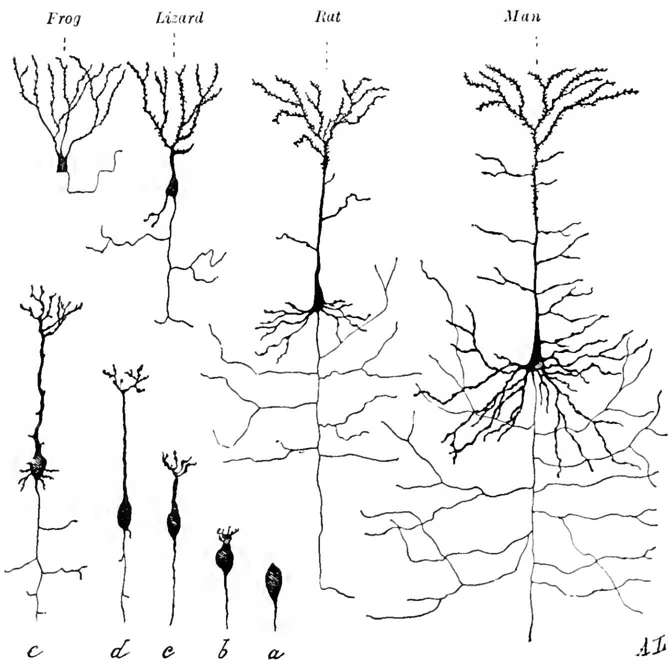


FIG. 178.—Phylogenetic and ontogenetic evolution of the pyramidal cell.

Pyramidal cell in the frog, the lizard, the rat, and in man.—*a, b, c, d, e*, progressive phases of embryological development of the pyramidal cell (after Cajal).

whose ascending axis cylinder mounts as far as the molecular layer, in which it spreads out longitudinally.

The cortex is thus strewn with cells and traversed by fibres. Of these fibres some are called radial and are of the nature of axis cylinders of pyramidal or analogous cells, and others are named *tangential* fibres. Amongst the radial fibres some are of great importance. These do not emanate from the cells of the cortex, but, on the contrary, from the subjacent regions of grey matter (particularly of the bulb and the spinal cord, grey nuclei, etc.) whose axis cylinders are represented by them. These fibres, after a journey of greater or less length, expand in the cortex up to the molecular layer, and come into contact with the dendrites of the pyramidal cells. These are *ascending* elements or, in other words, *sensory*.

The tangential or transverse fibres are those which, cutting the cortex in a direction perpendicular to the preceding, mark out by their larger or smaller number the strata which at certain points are visible to the naked eye. Some of these are axis cylinders proceeding in a transverse direction ; others, again, are the arborizations of axis cylinders, collaterals of great length, like those which have been described by Cajal as passing through the corpus callosum to the opposite hemisphere.

To all these elements may be added the fibres forming the neurogleia layer. etc., which, distributed amongst them, in ignorance of their true function, have been called supporting elements.

Local variations.—In the Rolandic convolutions an exaggerated development of the pyramidal cells has been observed (giant cells of Betz and Mershejewski). The body of the cell is here found to be developed in proportion to the great length of the axons, some of which descend as far as the sacral region of the spinal cord ; this development is most considerable in the paracentral lobule.

The occipital lobe is distinguished by a diminution in the number of its striae, and also by the exaggeration of one of the latter which gives origin to the stripe named after Vicq d'Azyr or Gennari. The cortex of this lobe is rich in tangential fibres ; its molecular layer is, on the contrary, reduced and its pyramidal cells diminished in number.

An exaggerated development of certain tangential fibres may also be observed in the insula ; the anterior wall and the amygdaloid nucleus must be considered as portions of the cortex enveloped in the white substance.

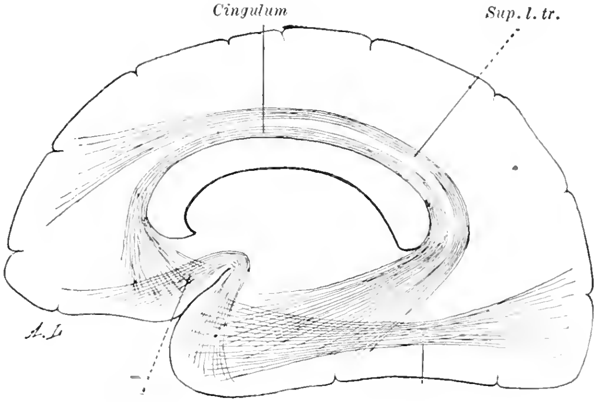


FIG. 179.—Diagram of the principal tracts of association seen by transparency (diagram, Charpy).

Course of the impulse.—These structural details supply us with explanations, if not about the precise progress, at any rate concerning the general course of cerebral functional processes.

The radial axis-cylinder fibres which distribute their terminations in the different layers, and more particularly in those of the pyramidal cells, are the ascending paths which carry to these cells impulses collected in the grey bulbo-medullary axis, where their cells of origin and their polar receptive field are situated. The radial fibres which arise

from the pyramidal cells and direct their axis cylinders towards the corona radiata, are, conversely, those which carry off the impulses from the brain to the grey bulbo-medullary axis. These are the fibres which, on account of their great length, are called *fibres of projection*, because the impulse is projected by them to a great distance, being conveyed from the inferior to the superior stratum of the nervous system, or reciprocally.

The fibres of the corpus callosum which unite the two hemispheres, the longitudinal fibres which join important or distant lobes in each hemisphere, and the tangential fibres which unite the convolutions which are more or less near to each other, are called fibres of association. This name has been given them because they associate distinct and determinate areas of the brain in a common function during the performance of complicated cerebral acts. Amongst these language may be brought forward as an example, for in this case several senses—hearing or sight—may alternately or simultaneously take part in the production of a motor phenomenon of great significance, such as speech or writing. Still shorter fibres, following either a radial, tangential or varied direction, belonging to these local cells of association, effect connexions between the neighbouring polar areas for the performance of more elementary actions.

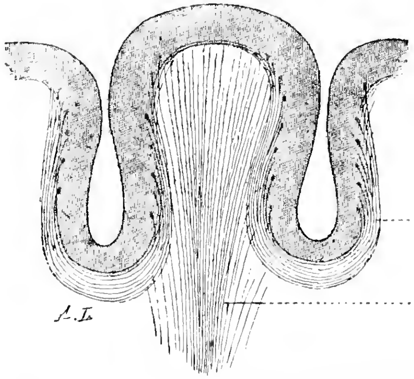


Fig. 180.—Diagram of the arrangement of the fibres of projection and the fibres of association (Charpy).

Varied collections of cells, extending from those which arise by the local association of two or three cells, up to those which bring into play large regions of the cortex, and at the same time render available long tracts in the sensori-motor paths, are thus found prepared as tactical units of a superposed and variable order, which are rapidly organized or dislocated by the progressive fusion of the cells or by their separation, in order to produce the formations corresponding to the very different acts which spring from the nervous functions.

Human brain.—We will assume a knowledge of the position of the fissures and the convolutions which indent the surface of each hemisphere, and which serve to divide it into arbitrarily limited areas, to each of which names have been given for the purpose of identifying and recognizing each individually in case of an isolated lesion. We will briefly call to mind the deep fissure (*fissure of Sylvius*),

which, at the base and laterally, separates the frontal from the temporal lobe, and by its posterior branch divides the parietal lobe from the temporal lobe; the *fissure of Rolando,* which, descending from the upper border of the hemisphere towards the Sylvian fissure, separates the frontal lobe from the parietal lobe, and the *perpendicular fissure* or parieto-occipital fissure (scarcely marked on the external surface), which separates the occipital lobe from the parietal lobe, and also (if prolonged in an imaginary manner) from the temporal lobe.

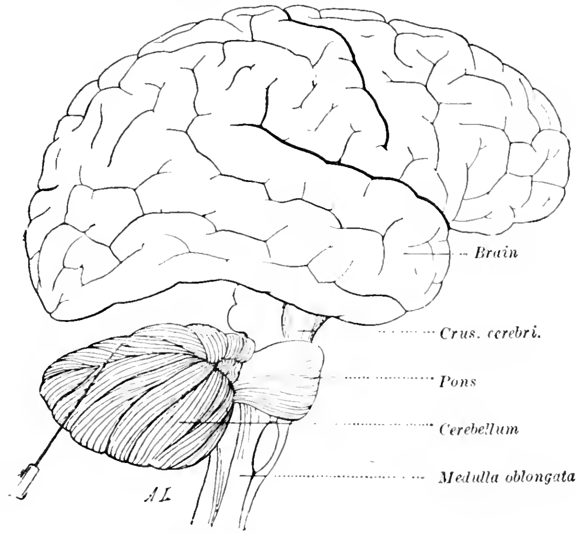


FIG. 181.—Human encephalon and its divisions.
Side view (copied from Schwalbe).

The convolution of the corpus callosum may also be observed on the mesial surface of the hemisphere; it is inflected on this great commissural tract and

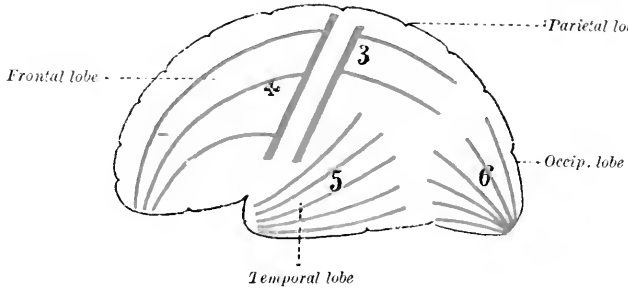


FIG. 182.—Diagram of the convolutions (after Charpy).
Their grouping and their general direction in man.

envelops it from its rostrum to its knee. The arch, open below, which it forms above the corpus callosum is closed beneath by the second temporal convolution. This convolution, after terminating in a hook towards the fissure of Sylvius, forms an almost closed crown round the hilum of the hemisphere. We may also notice the *limbic convolution* of Broca, whose relations to the olfactory tracts and olfactory bulb will be obvious. The remainder of the internal surface arranged

concentrically as a border round the convolution of Hill, forms the internal portion of the different lobes, whose limits are better seen on the external surface. Here may be found the internal frontal (internal part of the first frontal); this is prolonged behind the origin of the fissure of Rolando, by the paracentral lobe; it unites the two Rolandic convolutions which skirt along the fissure of that name. Then comes the *quadrilateral lobe or pre-cuneus*, an appendage of the first or superior parietal. Then between the perpendicular external fissure (parieto-occipital) and the calcarine fissure the *cuneus* belonging to the occipital lobe. Finally, lower down, we find the lingual lobe, a continuation of the second temporal, and the fusiform lobe, a continuation of the first temporal.

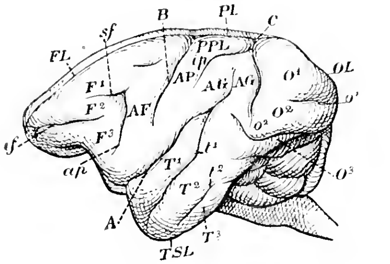


Fig. 183.—Brain of the dog-faced monkey (left hemisphere).

A, fissure of Sylvius; B, fissure of Rolando; C, parieto-occipital fissure; FL, frontal lobe; PL, parietal lobe; OL, occipital lobe; TSL, temporo-sphenoidal lobe.

F^1, superior frontal convolution; F^2, middle convolution; F^3, inferior frontal convolution; *sf*, supero-frontal fissure; *if*, infero-frontal fissure; *ap*, antero-parietal fissure; AF, ascending frontal convolution; AP, ascending parietal convolution; PPL, postero-parietal lobule; AG, angular gyrus or "*pli courbe*"; *ip*, intraparietal fissure; T^1, T^2, T^3, temporo-sphenoidal convolutions—superior, middle and inferior; t^1, t^2, superior and inferior temporo-sphenoidal fissures; O^1, O^2, O^3, superior, middle and inferior occipital convolutions; o^1, o^2, first and second occipital fissures.

It must be borne in mind that certain synonyms are employed. The convolutions which are grouped around the fissure of Rolando are called *central* convolutions. These, more than any others, have attracted the attention of physiologists and clinicians. The convolution by which this fissure is bordered in front is called *pre-Rolandic* or *ascending frontal;* and that bordering it behind, *post-Rolandic* or *ascending parietal.* From the first of these are given off in front the three *frontal* convolutions, the third of which has special importance; from the second, posteriorly, the *two parietal* convolutions. The two convolutions which border the posterior branch of the fissure of Sylvius are called *marginal;* the *supra-marginal* is none other than the *second* or *inferior parietal;* the *infra-marginal is the first* or *superior temporal.* The second or inferior parietal, sometimes called the supra-marginal convolution, which, being prolonged behind the fissure of Sylvius, twists round its extremity, also turning round the posterior extremity of the first temporal or infra-marginal convolution and, bending so as to retrace its steps, becomes continuous with the first temporal and forms the *pli courbe* (angular gyrus), an equally remarkable area of the brain and one often referred to in cerebral lesions.

Brain of the primates: monkey.—The brain of the monkey is sufficiently like that of man for the divisions adopted in the case of the latter to be recognizable with tolerable facility in that of the former. The same nomenclature may also be used in both cases, at any rate to designate the broader features. The fissure of Sylvius, the fissure of Rolando, the perpendicular internal fissure (parieto-occipital) continued externally by a perpendicular external fissure, no longer imaginary but strongly marked, divide the monkey's brain into four lobes (*frontal, occipital, temporal, parietal*), all very distinctly defined. Furrows divide these lobes into convolutions, of which some are easy to identify: the ascending frontal, bounded in front by the arched furrow (pre-central), the three other frontals indicated in a confused manner, and the inferior parietal, also clearly bounded above by the inter-parietal furrow. The insula is well developed.

The striated monkey, on account of its small size, is lissencephalic. The anthropoids (ourang-outang) have a third frontal convolution which is easily recognizable.

Brain of the carnivora : dog.—The brain of the dog, which is frequently experimented upon, and taken as type of that of the carnivora, requires a rather more detailed description, as the type to which it belongs differs notably from that of the primates and of man. This difference gives rise to great difficulties when the question arises of comparing the convolutions of each, either from a functional or a morphological point of view.

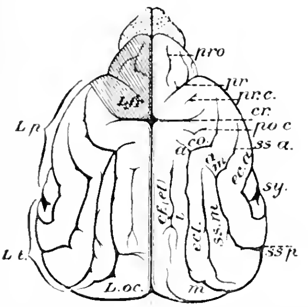


Fig. 184.—Brain of dog, superior surface ; lobes and fissures (after Ellenberger and Baum).

L.fr, frontal lobe ; *L.p*, parietal lobe ; *L.t*, temporal lobe ; *L.oc*, occipital lobe.

sy, fissure of Sylvius ; *ec.a*, anterior ectosylvian fissure ; *ss.m*, middle suprasylvian fissure ; *ss.a*, anterior suprasylvian fissure ; *ss.p*, posterior suprasylvian fissure ; *a.m*, small furrow " en anse " ; *c.o*, coronal fissure ; *m*, medio-lateral fissure ; *ef.(el)*, entolateral fissure ; *po. c*, post-cruciform furrow ; *cr*, post-cruciform fissure ; *pr*, presylvian fissure ; *pro*, superior frontal fissure (*fissura prorea*).

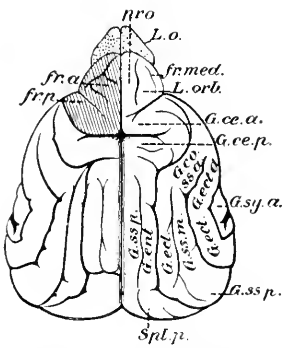


Fig. 185.—Brain of dog, superior surface lobes and convolutions (after Ellenberger and Baum).

L.o, olfactory lobe ; *L.orb*, frontal or orbital lobe ; *fr.a*, anterior frontal fissure ; *fr.p*, posterior frontal fissure ; *fr.med*, middle frontal fissure ; *pro*, superior frontal.

G.sy.a, anterior sylvian convolution ; *G.ect*, ectosylvian convolution ; *G.ect.a*, its anterior portion ; *g.ss.m*, middle suprasylvian convolution ; *G.co.* (*ss.a*), coronal or anterior suprasylvian convolution ; *g.ecl*, ectolateral convolution ; *G.ent*, entolateral convolution ; *G.ssp*, suprasplenial convolution ; *Spl.p*, posterior splenial convolution ; *G.ce.p*, central posterior convolution (post-Rolandic) ; *G.ca*, central anterior convolution (pre-Rolandic).

Superior surface.—*Sulci.*—The superior surface of the dog's brain shows us at first sight a sulcus in the shape of a cross. This is the *inter-hemispherical fissure*, which is cut perpendicularly by the *crucial sulcus*, at the union of its anterior with its median third. The last-named is the equivalent of the fissure of Rolando.

When the contour of the hemispheres is followed, the superior extremity of the *fissure of Sylvius* is found to be situated laterally and a little posteriorly ; this has the same signification in animals as in man.

The fissure of Sylvius is bordered by several sulci and concentric convolutions arranged in the form of a horseshoe.

These are (1) the fissure of Sylvius itself ; (2) the ectosylvian fissure ; (3) the suprasylvian fissure ; (4) the lateral fissure. This last is prolonged in front by the coronary fissure and another less important bifurcation, the furrow " en anse."

On the other hand there may be observed, between the crucial furrow and the coronary fissure, a small furrow (post-crucial) ; and in front of the crucial

furrow a more important furrow (pre-crucial); lastly, in front of this one two other small perpendicular furrows which form the boundary of three convolutions at the extremity of the frontal lobe.

Convolutions.—Immediately around the fissure of Sylvius, and, as it were, folded on itself, is the Sylvian convolution (consequently situated between the fissure of Sylvius and the ectosylvian fissure). Around this is the ectosylvian convolution (between the ectosylvian fissure and the suprasylvian fissure). The space between the suprasylvian fissure and the lateral fissure is subdivided at its median part into two convolutions by a furrow (the ectolateral furrow). These two are called the suprasylvian and the ectolateral convolutions. The space situated between the lateral fissure and the inter-hemispherical fissure is also subdivided by a furrow (ectolateral furrow) into two convolutions, namely: the suprasylvian and the ectolateral convolutions.

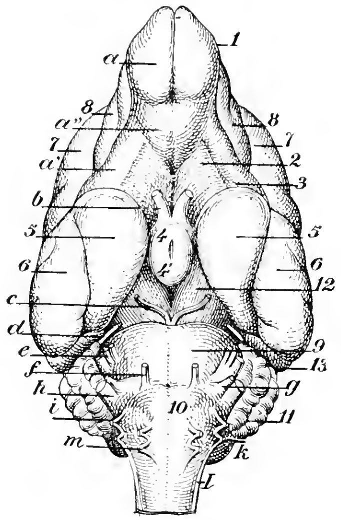


Fig. 186.—Brain of dog, its base, its appearance as a whole, and its lobes (after Ellenberger and Baum).

a, olfactory bulb; *a'* external branch, and a'', internal branch of the olfactory nerve; *b*, optic nerve; *c*, oculo-motor nerve; *d*, pathetic or trochlear nerve; *e*, trigeminal; *f*, external oculo-motor nerve; *g*, facial; *h*, auditory; *i*, glosso-pharyngeal; *k*, pneumogastric; *l*, spinal accessory; *m*, hypoglossal.

1, olfactory lobe; 2, anterior perforated space; 3, transverse tract along the anterior extremity of the pyriform lobe; 4, infundibulum; 4', corpora quadrigemina; 5, pyriform lobe; 6, temporal lobe; 7, parietal lobe; 8, frontal lobe; 9, pons; 10, rachidian bulb; 11, cerebellum; 12, crura cerebri; 13, occipital lobe partly seen.

These different sulci and convolutions are of tolerably large extent; in each and all a median portion, an anterior portion and a posterior portion may be observed, according to the position occupied by these parts in the horseshoe which they delineate around the fissure of Sylvius.

The fissure of Sylvius is, as is obvious, a very definite mark for the description of furrows and convolutions of the brain's surface, which surround it in a quadruple or even sextuple circuit. The crucial furrow, or fissure of Rolando, serves equally well to point out very important regions. Immediately behind it is the post-Rolandic or posterior central convolution; immediately in front the pre-Rolandic or anterior central convolution. The first of these answers to the ascending parietal, and the second to the ascending frontal in man. In front of the pre-crucial furrow which bounds the pre-Rolandic convolution, are three prolonged convolutions following the long axis of the brain and which are more or less equivalent to the three frontal convolutions.

Insula.—At the bottom of the fissure of Sylvius is an *insula* but little developed, consisting of two slightly marked folds.

Many authors, amongst whom Broca must be reckoned, do not regard the fissure of Rolando as the transverse branch of the crucial furrow, but as the pre-crucial furrow itself passing downwards to join the fissure of Sylvius. This view is supported by Eberstaller, who bases his opinion on the fact that the relations of the pre-crucial furrow with the insula are the same as those with the fissure of Rolando in the primates. Whatever be the value of such reasoning, which, even

from a morphological point of view is not particularly definite, it would be difficult in a work on physiology not to take into account the functional characters of the sulci and gyri so as to compare them with those of man and the primates. Therefore, from this point of view, the crucial sulcus is incontestably the centre

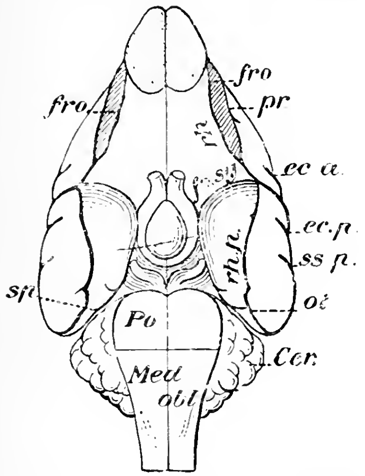


FIG. 187.—Brain of the dog, lower surface; lobes and fissures or furrows (after Ellenberger and Baum) (*).

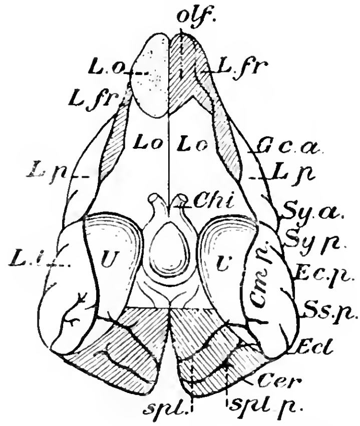


FIG. 188.—Brain of the dog, lower surface; lobes and convolutions (after Ellenberger and Baum) (**).

(*) *rh*, rhinal fissure; *ec.a*, anterior ectosylvian fissure; *ec.p*, posterior ectosylvian fissure; *ss.p*, posterior suprasylvian fissure; *sy*, fissure of Sylvius; *rh.p*, posterior rhinal fissure; *s.p*, splenial fissure; *o.t*, occipito-temporal fissure; *fo.sy*, sylvian fossa; *p.r*, pre-sylvian fissure; *fro*, frontal lobe; *Po*, pons; *med.obl*, medulla oblongata; *Cer*, cerebellum.

(**) Olfactory lobe removed from one side to allow the olfactory fissure to be seen. Cerebellum removed.

L.o, olfactory lobe; *L.fr*, frontal lobe; *L.p*, parietal lobe; *L.t*, temporal lobe; *Cer*, cerebellar surface of the hemispheres marked by dark lines; *U*, uncus or hook of the hippocampus; *Chi*, chiasma of the optic nerves.

G.c.a, anterior compound furrow; *Sy.a*, anterior portion of the fissure of Sylvius; *Sy.p*, its posterior portion; *Ec.p*, posterior ectosylvian fissure; *Ss.p*, posterior suprasylvian fissure; *Ecl*, ectolateral fissure: *Cm.p*, posterior compound fissure; *olf*, olfactory fissure (on the right of the diagram); *spl*, splenial fissure; *spl.p*, post-splenial fissure.

of the excitable region in the dog's brain (sigmoid gyrus), as the fissure of Rolando is in that of man. Hence arises the name of *central convolutions* applied indifferently in man and in the dog to the convolutions grouped, in the first named, around the fissure of Rolando; in the second, around the crucial sulcus.

Inferior surface.—*Sulci.*—The inferior surface, in addition to the interhemispherical fissure, shows us the origin of the fissure of Sylvius (*Sylvian fossa*) much widened. and which, when its borders are separated, allows the insula to be seen. The fissure of Sylvius, in its progress to the inferior surface of the hemisphere, is cut by a furrow extending from the apex of the frontal lobe as far as the occipital lobe: this is the *rhinal fissure*. This fissure bifurcates at its posterior extremity into two furrows, the external of which is named the *occipito-temporal* fissure, and the internal the splenial fissure. These fissures are indicated on the cerebellar aspect of the hemisphere. Behind on the same aspect is the *post-splenial* fissure.

Convolutions.—The fissure of Sylvius separates the pyriform lobe (an important portion of the temporal lobe to which belongs the *uncus* or hook of the hippocampus) from the parietal and olfactory lobes which are anterior to it. The

rhinal fissure in its anterior portion separates the olfactory from the frontal lobe ; and a little farther on it separates the olfactory from the parietal lobe. Later, it divides the pyriform lobe into two portions, leaving the uncus inside. On the lateral borders of the pyriform lobe and of the parietal lobe may be seen traces of the furrows and convolutions of the circumference.

Lateral surface.—The lateral surface displays to us these furrows and convolutions of the circumference delineated around the extremity of the fissure of Sylvius. It further displays, below, the rhinal fissure in its whole length ; above, the crucial furrow, the post-crucial furrow, and the pre-crucial furrow, which joins the rhinal fissure below. All along this furrow and the posterior part of the rhinal fissure is a space which separates these two fissures from the extremities of the convolutions of the circumference. This, proceeding downwards and posteriorly, is called the sigmoid convolution ; anteriorly, the composite convolution, and (behind the fissure of Sylvius) the posterior composite convolution.

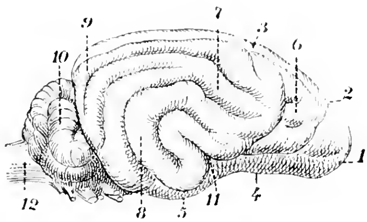


FIG. 189.—Brain of the dog, external surface ; its appearance as a whole and its lobes (after Ellenberger and Baum).

1, olfactory bulb ; 2, its boundary by the frontal lobe ; 3, boundary of the frontal and of the parietal lobes ; 4, olfactory tract ; 5, pyriform lobe ; 6, frontal lobe ; 7, parietal lobe ; 8, temporal lobe ; 9, occipital lobe ; 10, cerebellum ; 11, boundary between the parietal lobe and the temporal lobe (fissure of Sylvius) ; 12, medulla oblongata.

Internal surface.—The internal surface is divided into two bent parallel bands (almost as in man) by a long fissure which is itself bent round and slightly suggests the calloso-marginal fissure. At the internal part of the frontal lobe, this furrow bears the name of *fissure of the knee of the corpus callosum ;* at the level of the other lobes it is called the *splenial* fissure. The splenial fissure is really nothing else than the crucial sulcus, which, from the superior surface of the hemisphere, descends along the internal surface, then twists back so as to skirt the corpus callosum at a distance in the same direction, just as the furrow of the corpus callosum turns round it in front. The space separating it from the corpus callosum is the *convolution of the corpus callosum ;* but below the rostrum of this body it becomes the *convolution of the rostrum of the hippocampus* (*gyrus uncinatus*). The space comprised between it and the border of the hemisphere bears successively the following names : *subrostral* convolution (inferior part of the orbital lobe), *superior frontal* convolution (anterior part of this lobe), and *presplenial* convolution behind the crucial sulcus. Further back, the margin is subdivided by a fissure parallel to the splenial fissure into a splenial convolution and a suprasplenial convolution.

Limbic convolution.—The internal surface in the dog (as in all osmatics) is remarkable for the great development of the *limbic convolution,* and its very definite relations with the olfactory lobe. According to Broca, under the name of " limbic convolution " is described the convolution in the shape of a ring or a limbus, which is formed by the convolution of the corpus callosum (supracallosal portion) and the convolution of the hippocampus (subcallosal part of the limbic convolution). The ring gives passage to the corpus callosum and to the crus cerebri. Closed posteriorly by the welding together of the two sub- and supracallosal convolutions, it is in front closed by the olfactory lobe, which sinks in it its two strong roots, the outer one in the first, and the inner one in the second, and then continues it in front as an appendage. The relations of the whole of this apparatus with the sense of olfaction in the dog (and osmatics)

being admitted, it may collectively be designated either by the name "limbic

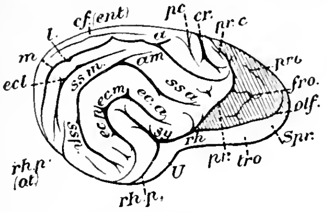


Fig. 190.—Brain of the dog, external surface; fissures (after Ellenberger and Baum) (*).

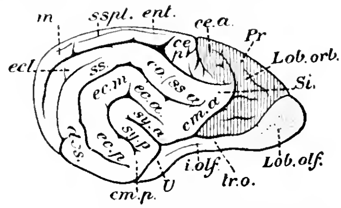


Fig. 191—Brain of the dog, external surface; convolutions (after Ellenberger and Baum) (**).

(*) *Pro*, superior frontal fissure; *spr*, subrostral convolution; *fro*, frontal fissure; *olf*, olfactory fissure; *rh*, rhinal fissure; *rh.p*, posterior rhinal fissure; *pr*, presylvian fissure; *pr.c*, precruciform fissure; *p.c*, post-cruciform furrow; *cr*, cruciform fissure; *sy*, fissure of Sylvius; *ss.m*, middle suprasylvian fissure; *ss.a*, anterior suprasylvian fissure; *ss.p*, posterior suprasylvian fissure; *ec.m*, middle ectosylvian fissure: *ec.a*, anterior ectosylvian fissure; *ec.p*, posterior ectosylvian fissure; *am*, small furrow "en anse"; *co*, coronal fissure; *ecl*, ectolateral fissure; *m*, medio-lateral fissure; *cf*, (*ent*), entolateral fissure (*fissura confinis*); *rh.p.(o.t.)*, posterior rhinal fissure and occipito-temporal; U, uncus; *tro*, olfactory lobe.

(**) *Lob.olf*, olfactory lobe; *Lob.orb*, orbital lobe; *Pr*, superior frontal convolution; *tr.o*, olfactory bandalette; U, uncus (pyriform apophysis); *ce.a*, anterior central convolution (pre-Rolandic); *ce.p*, posterior central convolution (post-Rolandic); *co.ss.a*, coronal convolution (anterior suprasylvian); *ec.a*, anterior ectosylvian convolution; *sy.a*, anterior sylvian convolution; *ec.m*, middle ectosylvian convolution; *ent*, entolateral convolution; *ss.pl*, suprasplenial convolution; *m*, marginal convolution; *ecl*, ectolateral convolution; *ss.p*, posterior suprasylvian convolution; *ss*, middle suprasylvian convolution; *sy.p*, posterior sylvian convolution; *iolf*, interolfactory fissure; *cm.p*, posterior composite convolution; *Si*, sigmoid convolution; *cm.a*, anterior composite convolution; *ec.p*, posterior ectosylvian convolution.

lobe," or else by that of "olfactory lobe," this latter name being, however, often reserved for its anterior enlargement.

Lobes.—The brain of the dog may be divided into four lobes more or less resembling those in man; and to these must be added, as in all osmatics, a fifth lobe, namely, the olfactory lobe.

The *frontal* lobe is separated from the parietal lobe by the crucial sulcus and its external prolongation; and from the olfactory lobe, outside by the rhinal fissure, and inside by the fissure of the knee of the corpus callosum.

The *parietal* lobe is separated from the temporal lobe by the fissure of Sylvius and its postero-superior prolongation.

The *occipital* lobe is bounded outside by the ectolateral fissure, behind and below by the splenial fissure; in front it has no definite boundary. The perpendicular internal and external fissures of the primates are here entirely wanting.

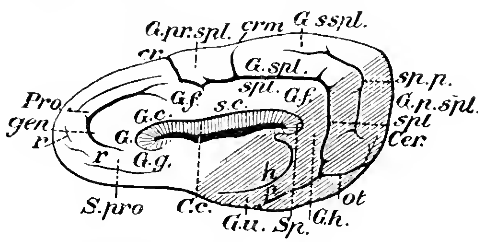


Fig. 192.—Brain of the dog, mesial aspect, convolutions and fissures (after Ellenberger and Baum).

Cr, cruciform furrow; *G.pr.spl*, presplenial convolution; *G.ss.pl*, suprasplenial convolution; *G.f*, convolution of the corpus callosum (*gyrus fornicatus*); *G.h*, hippocampal convolution; *G.g*, convolution of the knee of the corpus callosum; *G.p.spl*, post-splenial convolution; *G.c*, convolution of the cingulum; *G.u*, gyrus uncinatus; *G.u.p*, its posterior portion; *Pro*, superior frontal convolution; *S.pro*, subrostral convolution; *gen*, fissure of the knee of the corpus callosum; *spl*, splenial fissure: *Sp.p*, post-splenial fissure; *h*, fissure of the hippocampus; *s.c*, supracallosal fissure; *r*, rostral fissure; *crm*, small cruciform fissure; *G*, knee of the corpus callosum; *Sp*, splenium of the corpus callosum; *C.c*, corpus callosum; *Cer*, cerebellar surface of the brain; *ot*, occipito-temporal fissure.

The *temporal* lobe, interpolated between the two preceding lobes, is bounded, on the inferior surface of the brain, by the posterior rhinal fissure, which separates it from the lobe of the corpus callosum.

The *olfactory* lobe, prolonged backwards by the lobe of the corpus callosum, is separated externally from the frontal, temporal and parietal lobes by the rhinal fissure; from the occipital lobe, posteriorly by the splenial fissure; from the frontal lobe within, by the fissure of the knee of the corpus callosum.

The brain of the cat much resembles that of the dog, but, while in the dog the lateral convolution has its greatest development in the posterior region, in the cat the anterior region is the most developed. We may mention that, in the latter, the suprasylvian convolution containing the centre for the movements of the ears, is highly developed.

B. Corona radiata; internal capsule, crura cerebri.—From the grey medullary axis the impulse ascends to the cortex by a *direct* and *indirect* path, and redescends from it to the grey axis in the same

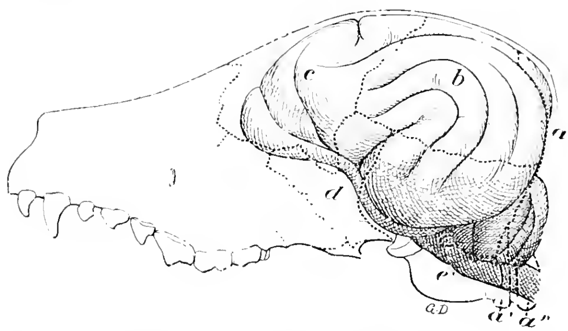


Fig. 193.—Relations of the convolutions to the sutures of the bones of the skull, in the dog (after Ellenberger and Baum) (*).

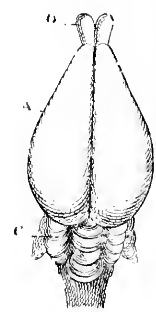


Fig. 194.—Brain of the rabbit (Lissencephalic). (**)

(*) *a*, occiput; *a'*, occipital condyle; *a''*, styloid; *b*, parietal; *c*, frontal; *d*, sphenoid; *e* temporal (squamous portion); *e'* tympanic bulba of the petrous portion.

(**) A, hemisphere; O, olfactory lobe; C, cerebellum.

manner. The crura cerebri formed by the fillet (*ruban de Reil*), enlarged by the sensorial and sensory elements which the medulla oblongata supplies to it (ascending path), and also by the pyramidal tract which is, in its turn, augmented by the geniculate tract (descending path), are the direct route and in every case contain it. The superior, median, and inferior cerebellar peduncles, which establish ascending and descending paths through the cerebellum between the grey axis and the cerebral cortex, are the indirect path. Other elements, also following an ascending and descending direction, furnish yet another indirect path through the basal ganglia (opto-striate bodies). This again follows the crura cerebri, and its fibres are arranged in a determinate area of the thickness of the latter. The direct fibres are found in the locality called that of the *crusta* (*pied*), and the indirect in that of the *tegumentum* (*calotte*).

The internal capsule is the layer of white matter which, being a continuation of the crura cerebri, extends to the cerebral cortex, intermingling its fibres with those of the corpus callosum to form the corona radiata. It marks out a passage in the centre of the hemisphere between the optic thalamus and the caudate nucleus, which are on its inner side, and the lenticular nucleus, which limits it externally. By moulding itself on the internal angle of the last named, it assumes the form of a capsule or of a dihedral angle, whose section has the shape of a set square, and whose apex, directed inwards, resembles the form of an elbow or a knee. The anterior limb of the angle is that which is called its anterior or *lenticulo-caudate* segment: its posterior limb is known as the posterior or *lenticulo-optic* segment.

The internal capsule, like the medullary roots, is a region which, on account of its relative structural simplicity, is of great interest to the physiologist and the clinician, and that interest is also aroused by the certainty and determinate character of the phenomena presented by its experimental lesion, and the equally relative simplicity of their interpretation.

The roots present themselves in the dissociated condition of conducting tracts devoted, the one exclusively to sensation (posterior roots), the other exclusively to motion (anterior roots). The internal capsule affords a new example of a like dissociation, with the exception that the bundles are here not distinctly obvious at first sight. Experimental or pathological lesions interrupting its posterior bundles produce a hemianesthesia of the opposite side; those interrupting its anterior portion produce hemiplegia, also crossed. At first sight it would seem as if this large layer of grey matter reproduced, by condensing it at the base of the brain, the sensory field which is distributed outside the spinal cord between the posterior roots and the *motor area* distributed between the anterior roots. Before giving a description of the important gradations by which they are distinguished from a functional point of view, it will be better to determine their relative position in a section of the capsule perpendicular to the general direction of its fibres.

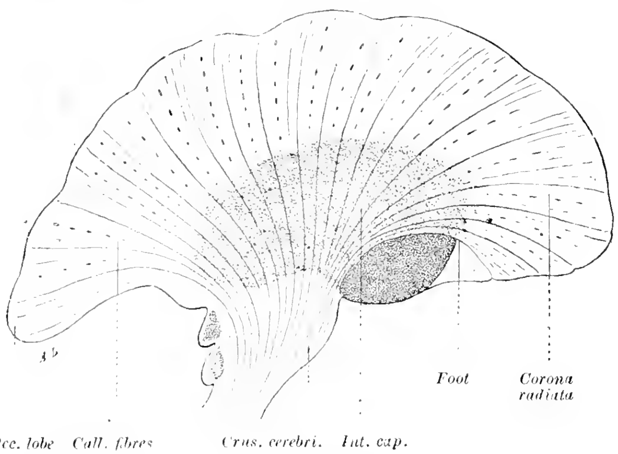


Fig. 195.—Diagram showing the internal capsule expanding in fan shape to form the corona radiata (diagram, Charpy).

The lenticular nucleus is seen on its internal aspect. The callosal fibres are dotted. The ganglia which interrupt the fibres of the occipital lobe are not represented (rad. opt.).

The *sensory tract* is contained in the posterior portion of the posterior or lenticulo-optic segment of the capsule; the *motor tract* is contained in the anterior part of this same segment up to and including the knee. The anterior or lenticulo-caudate segment of the capsule (in its anterior three-fourths) is a formation differing somewhat from the preceding, both as regards the direction of its fibres

and their initial and terminal connexions. This subject will be treated further on.

The sensori-motor area represented by the lenticulo-optic segment of the capsule is rendered noteworthy by the fact that it unites in a direct manner, though at the same time in a descending direction, the two most characteristic regions of the grey substance; namely, the grey bulbo-medullary axis and the cerebral cortex. It contains the fibres of projection which convey the impulse from one to the other in the two directions.

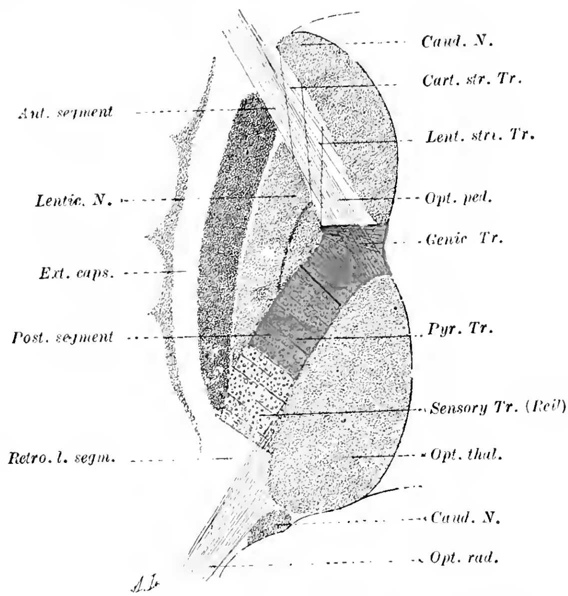


FIG. 196.—The left internal capsule, horizontal section.

Diagram of the tracts.—The motor tract and the sensory tract are supposed to be distinct.—The sensory path is not direct, like the motor path, but formed of fibres which are interrupted in the optic thalamus and again leave it in order to reach the cortex.

The motor area is subdivided anatomically into two tracts: the first, *cortico-medullary*, is adjacent to the sensory tract and is called *pyramidal* from the fact that, in traversing the medulla oblongata, it forms the pyramid of this organ (its second middle quarter answers to the superior limb, and its third middle quarter to the inferior limb). The second *cortico-bulbar* adjacent to the preceding, is called *geniculate* on account of its position in the knee of the capsule (it corresponds to the muscles of the face and of the tongue). These relations of the cortex with the spinal cord and the medulla oblongata do not involve essential differences of function. But, further, other fibres, distributed amongst the preceding without forming distinct bundles, descend from the cortex and proceed to the nuclei of the pons. These are the *cortico-pontine* fibres; they represent a particular kind of motricity, namely: the movement of the head and the eyes.

The sensory area is continuous with the medullary and bulbar nerves of general sensation. Further, in the bulb it becomes enlarged by the addition of elements representative of two new senses: taste (terminal nuclei of the glosso-pharyngeal) and hearing (nuclei of the cochlear and vestibular nerves). The fibres conductive of visual and olfactive sensation remain outside the path of the internal capsule, joining the cortex by individually independent paths.

Thus constituted the sensory tract of the capsule is none other than the fillet (*ruban de Reil*), an assemblage of *medullary* and *bulbo-cortical* fibres which have their origin in regions of grey matter morphologically differentiated from the grey axis, and their terminations in distinct areas of the cerebral cortex.

Cortical fillet (ruban de Reil).—The sensory field is thus in a certain sense comparable to the motor field. Two neurons, one external, the other deeply

situated, form the essential woof of the former as well as of the latter, and on this woof are woven, so to speak, innumerable complications. However, this apparent agreement conceals extremely important differences. One of the most weighty of these is the following : just in the same proportion as the relations of the motor field to the cortex are obvious, so are those of the sensory field little marked ; and conversely as regards the optic thalamus, those of the first are diffuse and little characterized, while those of the second are obvious.

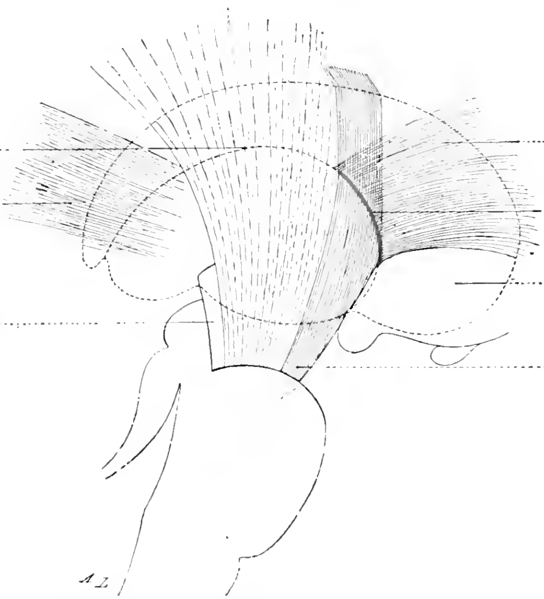


FIG. 197.—Principal bundles of the internal capsule, and of the corona radiata (after Charpy).

Left hemisphere seen on its mesial surface. The caudate nucleus and the optic thalamus whose outline is marked in, have been removed by scratching. The red line indicates the extent of the genu. The bundle of Meynert, which is at the same time external and posterior, is inflected in order to proceed to the temporal region ; so also is the geniculated tract, internal and anterior in order to reach the base of the Rolandic convolutions. The anterior segment is wanting below, the corpora striata being fused together.

Under the name of cortical fillet (cortical ruban de Reil) the existence is maintained of neurons of all lengths, these being the counterpart of the pyramidal and geniculated bundles of the motor field ; they are present in but small proportion. Under the name of thalamic fillet (ruban de Reil de thalamique) well defined tracts are described relatively, which stop and are reinforced in the ventral part of the optic thalamus before being carried on by other neurons from it to the cortex (Monakow, Hösel, Mahaim, Flechsig).

In addition to these *medullo-* and *bulbo-cortical* elements, the internal capsule is complicated by the presence of *medullo-* and *bulbo-thalamic* elements, principally sensory, and also by *thalamo-cortical* elements duplicated by fibres of contrary direction, without taking into account the analogous relations of the corpus striatum, and those of these different ganglia amongst themselves. Anatomo-clinical facts designate the optic thalamus and its thalamo-cortical riband

(fillet) as the path most essential to sensation. *Hemianæsthesia* caused by lesion of the internal capsule is never observable except when the optic thalamus is itself injured (portion situated in front of the pulvinar), or when the thalamo-cortical riband (fillet) is interrupted (Long, Thése de Paris, 1889).

Experiments.—As it is known that the capsule represents an assemblage of conductive fibres of very different functions, these fibres have been experimentally interrupted in a more or less isolated manner.

Compared with that of the posterior roots, the section of a sensory tract is followed by the same effects, which are immediately and markedly apparent. *Conscious* sensibility is abolished in the corresponding cutaneous territory; or, in other words, in the opposite half of the body (*hemianæsthesia*). In both cases an external excitation no longer reaches the cortex, its arrival thither being an essential condition for the realization of the phenomena of consciousness. In the case of section of the radicular sensory neurons (if it were possible to generalize it), every response to external excitation would become impossible, all the paths leading to the grey substance then being cut, and this substance being the place of distribution of this impulse among the motor nerves. The impulses which have previously reached the deep systems would alone be able to circulate there. In case of section of the sensory tract of the capsule, the impulses collected by the grey bulbo-medullary nuclei would give rise by their intervention to a *reflex* response which in the former case would be an impossibility; but the cortex would no longer receive any impulse, not even one of an entirely internal nature, from the grey medullary axis.

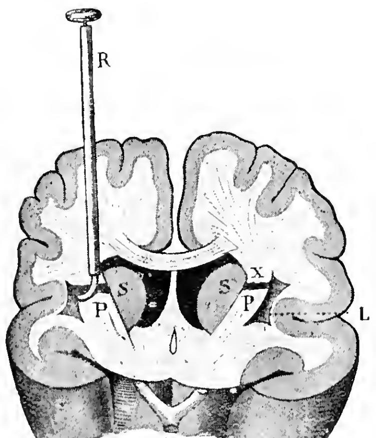


Fig. 198.—Experimental section of the internal capsule (experiment of Veyssières and of Carville and Duret).

SS, caudate nuclei of the corpora striata; L, lenticular nucleus; P, peduncular expansion of internal capsule; X, section of the peduncular expansion which produces hemiplegia; R, stylet with a spring for performing section of the internal capsule.

Veyssières, and especially Carville and Duret, have performed experiments with the object of separately cutting the component tracts of the internal capsule. To reach this deep white layer they employed a trocar provided with an articulated blade which, when once the instrument was sunk in the brain, could, by means of a spring, be manipulated from the outside through the wall of the skull. When

the section is made in the *posterior* portion of the internal capsule, hemianæsthesia occurs ; when in the *anterior* portion, hemiparalysis is the result. Yet certain reserves must be made in accepting these conclusions. Just in proportion as the distance from the roots is increased, and the cortex approached, so does any distinction between the elements of sensation and those of movement become more difficult to effect. Further, it is not possible to guarantee that the optic thalamus and its thalamo-cortical tract have not been damaged by the section. In both cases the results affect the opposite side of the body.

Crura cerebri.—When a transverse section of the crura cerebri is affected, two regions are distinguishable, the one that of the tegmentum (*calotte*) and the other the crusta (*pied*). The fibres in the region of the crusta arise directly from the cerebral cortex without any interruption in the central ganglia, and proceed from the median sector of the cortex, with the exception of the anterior and posterior regions (Dejerine). These fibres are *cortico-medullary* neurons (pyramidal tract), *cortico-bulbar* neurons (cerebral tract of the motor cranial nerves), *cortico-pontine* neurons (which are called the tract of Türck, and which must not be confounded with the direct pyramidal tract which bears the same name), and finally, *neurons proceeding from the cortex to the locus niger*. The radiations of the *locus niger* arise especially from the superior Rolandic regions ; they occupy chiefly the external two-fifths of the crusta of the peduncle. The cortico-pontine radiations proceed from all the median sector of the hemisphere ; they occur mostly in the internal four-fifths of the crusta of the crus cerebri.

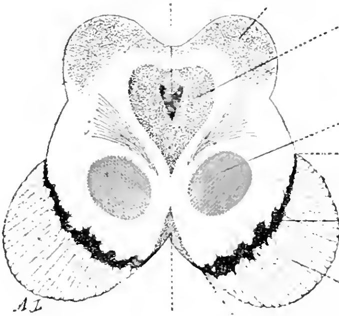


Fig. 199.—Section of the crus cerebri.

The crusta is separated from the tegmentum by the locus niger of Semering.

The cortico-medullary radiations arise from the Rolandic operculum and from the adjacent portion of the frontal operculum ; they traverse the knee of the internal capsule and occupy the internal tract of the crusta of the crus cerebri.

The cortico-medullary radiations arise chiefly from the superior three-quarters of the Rolandic region. They pass through the posterior segment of the capsule between the knee and the retro-lenticular segment and occupy the middle three-fifths of the crusta of the cerebral peduncle, afterwards forming the bulbar pyramid.

These different radiations thus individually occupy certain regions in preference to others in the crus cerebri. But they do not form here separate tracts ; on the contrary, they are somewhat profusely intermingled both in the crusta of the peduncles and in the posterior segment of the internal capsule.

2. The psychical functions of the brain

The experiments of Flourens are of fundamental importance in the

history of the functions of the deep nervous system. They portray the question of localization in its broad outlines, as is desirable in commencing the subject. These experiments, considered from this point of view, give a solution the expression of which has not greatly altered. But this study is, and in fact could only be, a first approximation. The brain, with the conventional boundaries assigned it by anatomy, is not the organ of a functional localization abruptly arrested and which is superposed on these identical limits. On the contrary, it is attached, both anatomically and physiologically, to inferior systems, of which it is the elaborated expression.

Analysis, after having indicated the functional dissimilitude existing between the large segments of the encephalon, points out their analogy when it attacks them in detail, because it finds them in their turn to be formed individually of numerous systems of unequal value, these systems being in a state of transition from one to another.

A. Ablation of the cortex in mammals.—Everything tends to point out the grey matter of the brain as performing the most characteristic function of all those devolved on this organ. On account of its superficial position, and in spite of certain difficulties, this portion of the brain is the most accessible to experiment. What, then, we may ask, will be the modifications of the nervous, motor, sensory, sensorial, physical, etc., functions in an animal whose cortex has been removed as completely as possible ?

1. **Scheme of the experiment.**—The leading idea of the experiment was to leave intact all the organs of the senses in connexion with the grey sub-cortical masses, but to entirely destroy the cortical matter itself, and then, by the modification thus induced, to infer the functional value of the cortex which has been removed.

Goltz was able to carry out this experiment on a dog and afterwards to keep the animal alive during eighteen months. The project was, however, only approximately realized ; but, nevertheless, as far as it goes, in an adequate manner.

Operative results.—The removal of the cortex (effected in several operations) was not entirely complete. It was necessary to spare the uncus on both sides so as not to injure the optic nerves, therefore a portion of the cortical gustatory area remained. On the contrary, the external geniculate body was involved on the left side, which entailed a degeneration of the anterior corpus quadrigeminum and of the corresponding optic thalamus. The sub-cortical visual apparatus was thus destroyed on one side, but retained on the other as a control of the visual functions (there was persistence of the pupillary reflex to light). The olfactory lobes were in part retained. It must be noted further that the removal of the cortex gave rise to secondary degenerations in the corpora striata and the optic thalami, both of these being attacked with softening.

Great care was taken at first to forcibly feed the animal, as it refused all nourishment, and only began to accept it on the twenty-third day.

State of the senses.—The sensory and sensorial functions in this animal did not completely disappear ; in fact, on a superficial examination, they might have been considered to have been preserved. The animal closed its eyes at the approach of a bright light ; a paw brought into contact with cold water was instantly withdrawn. Pinching of the skin, insufflation of air into the external ear or over the eyes provoked defensive movements. Annoyed by such stimulations, the animal barked, growled, and tried, but unsuccessfully, to bite. A loud and prolonged noise awoke it, and even provoked defensive movements. Nothing definite was noticed concerning the sense of smell ; but food, accepted and swallowed if it had its normal qualities, was rejected when impregnated with a bitter substance. When its fast was prolonged, the animal walked without cessation in all directions in its cage, putting out its tongue in a rhythmical manner. When its food was put in front of it, it drank, ate, and, once its hunger satisfied, slept.

Nutrition.—The quantity of food necessary to maintain it in good condition was considerable, 1,000 grammes of meat and 500 grammes of milk for a dog weighing 5 kilos. A rather large loss occurred by the fæces ; and, on the other hand, the skin was generally very warm, indicating that the animal lost large quantities of heat.

The urine was normal ; the excreta had the usual appearance. Digestion and the functions of nutrition in general were carried on in the normal manner.

Instincts, emotions.—The sexual instinct was destroyed. The animal did not of itself show any emotion, either gay or sad ; it did not answer by any sign to caresses, menaces, calls, or to the sight of other animals.

2. **Earlier experiments.**—This description differs from that which is usually given of an animal deprived of its cerebrum, according to the account of Flourens. Nevertheless, the principal features persist, and the resemblance is maintained, thanks to some re-touching. Like the pigeon described by Flourens, the dog of Goltz deprived of its cerebrum does not seek its food for itself, even when it is pinched by hunger ; it merely accepts it when placed before it. The principal instincts, the emotions, the intelligence properly so called, have disappeared. The movements, unquestionably very complicated, *that the animal deprived of its cerebrum is capable of performing have hardly any spontaneity ;* they are the response to an immediate provocation, consisting in external excitations of the senses of hearing, sight and touch . . . or in internal excitations of the kind to which hunger gives rise. It is

remarkable that, under the influence of these latter, the animal performs all the movements requisite for nutrition, including the prehension of food.

Psychical images.—After removal of the cortex, the animal completely loses the benefit of those anterior impulses slowly warehoused and preserved by the brain under the form of what are called cerebral images. These cerebral images, persisting in the mind after the withdrawal of the object, superpose themselves on the present or actual image of that object, and, being mutually associated in different ways and circumstances, end by attributing to it a symbolical, that is to say, a synthetic value. The crack of a whip will draw cries from the animal, and will provoke reactions of a defensive nature ; the sight of the whip will make no impression upon it, because it no longer awakens the image or remembrance of anterior sensations experienced by means of this same object.

Not only is the store of co-ordinated impulses under the form of acquired knowledge or complex images annihilated, but the power of re-acquiring knowledge of the same nature no longer perceptibly exists. For months the animal deprived of the cerebrum may be taken out of its cage at the time of meals, and for months this manipulation will provoke its anger, because it is incapable of recognizing a connexion between the action and the meal which it desires, or the hunger from which it suffers.

Partial re-education.—However, though the animal is condemned to profound and irremediable decadence, yet facts tend to show that it is nevertheless susceptible, in a small measure, of a partial re-education as regards those nervous functions which are the most directly connected with nutrition. Immediately after the operation deglutition is extremely difficult, and prehension of food is abolished. These two functions, however, are in the end normally performed ; the former being first re-acquired, and the latter at a later date. This indicates the culminating point in the secondary education of the animal. The mechanism by which these faculties are re-acquired is capable of several explanations. There may have been merely an arrest of the functions of the sub-cortical nervous masses caused by the shock of the operative lesion ; this hypothesis is the one to which Goltz gives his adhesion. According to this author, it may be possible that the functions of those masses which are phylogenetically and ontogenetically anterior to the brain itself, and which, for this reason, have at first performed the cerebral functions, but which in the developed animal are only exercised in concert with the brain and under its direction, may, by means of the repetition of excitations terminating in them, re-acquire their

primitive development and once more take upon themselves the function of directive systems, after the loss of those from which they had previously received this direction.

In any case the conclusion to be drawn is that, in order to explain the aptitudes retained by the animal after the loss of its brain, it should be examined not only in the days immediately following the operation, but again after as long a delay as possible ; it being probable that the results obtained after this delay will notably differ in some respects from those previously observed.

3. **The cerebral cortex and sensation.**—In the animal deprived of its cerebrum stimulation of the senses provokes co-ordinated responsive movements, these, however no longer having the value of what, in ordinary language, are called intelligent, or even instinctive acts, but displaying nevertheless a marked adaptation to the stimulation itself. This adaptation is so striking that the movements have been named defensive reactions. Are these excitations *felt?* Quite lately the nervous phenomena of the reception of impulses were divided into two categories, the characteristic of the one being the sensation by which they were accompanied ; and of the other, the absence of that sensation.

The nervous act in the first case is conscious-voluntary ; in the second it is called reflex or automatic, and by this is meant that its nature remains entirely *mechanical*, while in the first it has a psychical character. Further, the doctrine seems pretty firmly established that nervous phenomena must belong either to the first or second of these two categories, according to their localization either within or outside the cerebral cortex.

Cortical reflexes.—This expression is much too simple, and, above all, too exclusive. The participation of the cortex is doubtless necessary in acts of an evident and well-defined psychical character. This is explained by the fact that, owing to its predominant situation and its complicated structure,-the cortex alone is adapted to the realization of these phenomena of synthetic nature, no other region of the grey matter being capable of effecting this synthesis in the same degree. But this aptitude does not exclude it from participation in phenomena of a simpler and apparently automatic or reflex order. Everything depends on the number, the value, or the individual complexity of the systems which are associated for the performance of the act to be carried out, this act being either of a simple nature, such as the winking of the eyelids, or proceeding gradually upwards in the scale until a complicated action, such as premeditated speech, is attained. All these acts, though of such unequal value, may imply the participation of the cerebral cortex.

The sub-cortical systems.—The sub-cortical systems take part in a large number of apparently automatic and reflex acts, which they are capable of performing without the aid of the cortex. The determination of this fact has been the origin of a generalization resembling the preceding one; reflex phenomena have therefore been attributed to these systems in almost as exclusive a manner as consciousness has been reserved for the cerebral cortex.

Gradation of the psychical phenomena.—So absolute an opposition is justified neither by the facts of anatomy nor of physiology. The authentication of nervous acts, some quite rudimentary, while others have attained their greatest development, ought not to cause us to forget the intermediate series connecting the first with the second. It is the acts belonging to this state of transition which are brought into strong relief by the experiment of Goltz.

4. **Sensations which have undergone reduction.**—Sight, hearing, touch and taste in an animal deprived of its cerebrum are certainly considerably *reduced*, compared with the acuteness of these senses in the normal animal. We may add, that it is difficult to say which elements belonging to each of these senses have suffered this reduction; but, as Goltz remarks, it would be still more difficult to deny sensations to an animal in this condition, since the criterion which we employ to authenticate them in animals in a normal state, that is to say, special motor reactions (specific in a sense) by means of which they are revealed to us, still persist in it. Intelligence, knowledge, instinct, are complex facts, into which sensations enter as component unities or, as they are sometimes called, elements. This element itself is not a simple one, being produced as it is by functional associations which necessitate a systematization of the nervous cellular activities.

The experiment of Goltz, the removal of the cortex, brings into existence a systematization from which knowledge and intelligence have disappeared, but one that is still capable of developing crude sensation furnished with a character which endows it with a sufficient resemblance to the clear and highly differentiated sensation serving as a comparison. Further, this doctrine is not a new one. Longet and Vulpian noticed that, after the removal of the brain down to the pons, but not including the latter, a sensory stimulation may be followed by emotional reactions on the part of the animal thus mutilated, the character of these reactions having convinced them of the existence of a *crude* sensation which is quite opposed to that entirely conscious sensation, the development of which necessitates the intervention of the hemispheres. The experiment of Goltz, by allowing of the survival of the animal, is more striking and more decisive: it also lends itself

better to psychological analysis. And as it differs with regard to the destructions brought about, it serves to enlighten us still more as to the part played by the cortex in the functions of the brain.

B. Removal of the cortex in birds.—Removal of the cortex in birds (especially in the pigeon) has been, since the experiments of Flourens, repeated by Schrader and by Munck, who limited the destruction to the cortex and did not injure the basal ganglia. According to Schrader, and Richet held the same opinion, the results obtained by Flourens (motionless position and loss of special sensations) are due to the simultaneous destruction of the optic thalamus and of the cortex. When this latter alone is destroyed, the animal can still see, move, and avoid obstacles; this result is, however, contested by Munck, who thinks that in this case the loss of vision would be quite complete.

Instinct is lost. Movements are made only in response to immediate stimulations: they are no longer spontaneous. Differences of opinion, as noticed above in the case of the dog, exist chiefly as regards the persistence of sensations. They seem to arise, less from the variation in the *results* of experiment, than from the conceptions formed by different authors as to what is to be understood by sensation and the *criteria* which permit of its recognition.

C. Removal of the cortex in the frog.—According to Renzi, it is necessary, as Longet had already remarked, to distinguish in birds, amphibians and reptiles a mental vision requiring the integrity of the cerebral cortex, and a crude sensation of sight, for which the mesencephalon is sufficient. According to Schrader, not only would the visual sense be preserved, but, once the shock of the operation over, the animal would be able to change its place and its surroundings, according to the season, and to find its own nourishment by means of the flies which it catches. The instinct of the animal would here be retained as well as sensation. Centralization, which is well defined in superior animals, and which has placed the nervous system in dependence on the brain, has so far made but little progress in batrachia.

This can be proved by dividing the spinal cord into three segments by two sections, one of these represented by the head, the second by the superior limbs, and the third by the inferior limbs, each having an independent function.

The experiment of separating the encephalon and then arousing, by stimulation of the skin of the back, the reflex action of the spinal cord, is well known. The movements resulting from this stimulation are adapted and co-ordinated in such a way as to suggest a desire for the removal of these excitations: they are, in their own fashion, the response to the latter.

3. The exchanges between the brain and the blood

It is allowed, in principle, that the activity of organs is connected with an exchange, a waste (followed by a recuperation) of these organs. To define in what this change consists is the problem with which positive science is confronted. Only as regards some organs, amongst which the muscle may be particularly mentioned, has the solution of this problem commenced. The methods followed and the results obtained are models which have been utilized for the study of the functions of other organs, and particularly of the brain, which functions have up to the present time been almost incapable of explanation. This method is a legitimate one, provided that the conclusions arrived

at do not go beyond the compass of the facts. By experiments copied from those which have served to define the function of muscle, we may attempt to clear up those of the brain.

Cycle of energy in the muscle.—In the muscle, the leading idea of these experiments has been to follow through it a double current of matter and of energy, which, conveyed from the exterior, returns there after having formed part of the muscle. This current undergoes in it a kind of evolution, in which three principal phases may be distinguished (initial, intermediate and final). In each of these matter and energy, preserved in a constant quantity, assume characteristic forms, which answer the purpose of defining muscular function, at least as regards what is most essential to it. The value of experiments performed on the muscle arises from the fact that the ascertained results are not only qualitative, but also quantitative, and that the quantitative equivalence of the successive forms of energy guarantees its source and its connexion. In the muscle matter and energy first enter the muscle and then leave it transformed ; they enter it united and leave it dissociated. This dissociation of matter and of energy may even be regarded as being characteristic of the muscular function, as it is not found in the same degree in any other tissue. In the muscle, energy, in its initial or intermediate phase (at the time of its entrance, and when it is there stored up), is present in a chemical form. In its final phase (at the moment of its leaving the muscle) it is partly mechanical and partly thermic. *The function of muscle*, as it appears to us, *is essentially an energetic function.*

The very simple equation of the combustion of the blood's glucose in the muscle gives us information concerning both these mutations of matter and of the liberation of energy which occurs in this organ at the moment of its activity.

Energetic cycle of the brain.—In the brain, when we seek to establish a cycle of the same nature, we find several elements wanting. It may be that these are really in default, or, perhaps, merely that experiment has so far been found incapable of revealing them to us. In the final condition of this cycle there manifestly can be no mechanical operation ; with much difficulty it has been possible to ascertain in certain special conditions that there is a liberation of heat, which is manifested by an imperceptible elevation of the temperature. This is all that it is possible to grasp, by *direct* means, concerning the liberation of energy. If we wish, as in the muscle, to make *indirect* calorimetric measurements, that is to say, to ascend to the source of energy by formulating the chemical equation which can explain its production to us, we must take for a criterion the oxygen which is consumed in the muscle, and the carbonic acid which is produced therein, by measuring the quantity of these two gases in the blood which enters and in that which leaves the brain. Experiments of this nature have been performed by L. Hill and D. N. Nabarro ; they also tend to prove that the cerebral energetic waste of tissue is a very slight one. The table which follows shows the average results obtained from a certain number of experiments, giving the balance-sheet of the gaseous exchanges in the brain, and, by comparison, in the muscles of the inferior limb. Experiments have been made, on the one hand on the brain and the muscles in a state of repose, or at least after their activity had been diminished by morphia narcosis ; and, on the other hand, on the brain and the muscles thrown into a condition of hyper-activity by attacks of epilepsy provoked by means of an injection of absinthe or of strychnine. The blood was taken from the carotid and the torcula Herophili in order to estimate the exchanges in the brain ; from the carotid and the deep femoral vein in order to form an estimation of the changes in the muscle (arterial blood has the same composition in all arteries).

Comparison of the gaseous exchanges in the brain and the muscles in repose and activity

	BRAIN.			MUSCLE.			
Gas of the blood.	Carotid artery.	Torcula Herophili.	Difference.	Carotid artery.	Deep femoral vein.	Difference.	Reckoning the co-efficient of circulation.
			Normal state, or that of repose.				
CO^2 ...	48·85	44·74	+3·87	37·63	46·39	+ 8·76	
O^2 ...	16·81	13·39	−3·4	18·10	5·12	−12·98	
			3·64			10·84	×1=10·84
			Tonic phase of epilepsy.				
CO^2 ...	44·98	49·04	+4·06	39·53	53·43	+13·90	×3=41·70
O^2 ...	15·17	10·22	−4·95	17·05	3·30	−13·75	×3=41·25
			4·50			13·82	×3=41·47
			Clonic phase of epilepsy.				
CO^2 ...	30·59	33·58	+2·99	25·33	44·66	+19·33	×3=57·99
O^2 ...	15·77	11·46	−4·31	18·66	6·03	−12·63	×3=37·89
			3·65			15·98	×3=47·94
			Animal under morphia.				
CO^2 ...	37·6	41·65	+4·01	37·6	45·75	+ 8·1	
O^2 ...	18·25	13·49	−4·76	18·25	6·34	−11·91	
			4·38			10·00	=10·00

1. **Indirect calorimetry.**—Although we do not exactly know the nature of the oxidative process which makes use of oxygen in the brain and produces carbonic acid therein, indirect calorimetry bears witness, for its part, to the *small waste of energy* in this organ. However small this waste may be, it nevertheless has a special interest if we can only grasp the connexion by which it is attached to another aspect of the brain's function, namely, to the *psychical phenomena* which reveal its internal activity. But no parallelism between these two orders of phenomena can be ascertained. If (as it has been possible to do in the case of loss of substance of the skull) a sensitive thermometer is brought into contact with the cerebral cortex of a human being, it will not be found that the temperature is lowered during sleep, is raised in wakefulness, or is exaggerated during the most intense intellectual activity; *and, if oscillations present themselves, they arise without any necessary agreement with the variations of the psychical activity,* and sometimes in a sense opposed to that which has just been indicated. It has been possible to observe them during deep slumber. Occasion-

ally they have appeared to coincide with unconscious excitations of the senses (external noise, but not sufficient to cause awakening), and reveal rather an emotional condition than an act of comprehension, or an intellectual effort. In animals, elevation of the cerebral temperature is most marked when asphyxia is produced, and attains its maximum when consciousness has vanished. But it must be remarked that the thermometric effect is only obvious a certain time after the cause which produced it has ceased to act, and that death by asphyxia is preceded by a certain condition of over-excitement of the whole nervous system, including the brain (Mosso).

The elevation of temperature thus observed is correlative with the *total* activity of the cerebral region when thermometrically investigated; the phenomena that we call conscious only respond, on the contrary, to a *partial* activity of the brain. As a matter of fact, in the brain, including its cortex, unconscious run parallel with conscious phenomena, and it is impossible to separate one from the other, because conscious phenomena are alone perceived by us in virtue of the internal activity of the brain. Unconscious phenomena escape us, by the same definition. Further, the field of consciousness is not fixed, but may every moment become larger, or smaller, or be displaced (in waking, in sleep, in the different directions in which attention is occupied). It is thus obvious that *no common measure between heat and psychical activity can exist* ; or, in other words, between heat and the phenomena of psychological consciousness.

2. **Heat and thought.**—The hope has been entertained of finding, by the help of these experiments, an equivalence between the physical energy which our external senses perceive and the altogether internal phenomenon which we call psychical, precisely because it is perceptible to our internal sense alone. Whatever conception may be formed of one or the other, it may be seen that the problem is incapable of solution by experiment. We need not be too much surprised at this. Amongst physical phenomena heat is one of the simplest that we can discern ; on the contrary, the phenomenon called thought is one of the most complex we are capable of dealing with : they represent to us two opposite poles of phenomenality. It would not be possible for them to have a common measure.

3. **Cerebral circulation.**—The cerebral circulation, considered from a purely mechanical point of view, has been studied elsewhere (see *Circulation*, page 255) ; here we have to consider it in relation to the cerebral function itself.

The relations of mutual dependence existing between the heart and the brain are of a very obvious nature. They declare themselves in a

striking manner whenever one of these organs is disturbed, in the performance of its functions, by the reaction of this disturbance on the other.

a. *Action of the heart on the brain.*—A momentary stoppage of the heart has an immediate effect on the cerebral function, displayed by loss of consciousness (commonly called loss of the senses), insensibility, muscular flaccidity ; to these phenomena, taken as a whole, the name of *syncope* has been given. No organ preserves its excitability when deprived of its blood supply ; but while, as regards many organs, this loss of function is slow and gradual, requiring even hours for its full development, we see that in the case of the brain as regards its grey matter, and especially its cortex, this loss is, so to speak, instantaneous in warm-blooded animals. Experiment confirms this fact of every-day observation. Chauveau, while operating on the cranial nerves, noticed that sensation did not outlive the last beats of the heart. On the other hand, the excitability of the motor nerves is preserved for a certain time after death. Motor excitability is a cellular function. Sensation, in its conscious form, is a function appertaining to a complex systematization (brought into being principally in the brain). In the work of destruction which inevitably follows anæmia when pushed to its extreme limits, it is therefore the cellular elements which are primarily separated the one from the other ; ultimately disorganization invades these elements themselves, following a regular order.

b. *Action of the brain on the heart.*—The disturbances of brainfunction exert, on their side, a reactional influence on the functions of the heart. The influence of emotions or of different passions on the cardiac rhythm is well known. In some cases this rhythm is hastened ; in others it is slackened ; sometimes the psychical impression, if very keen, may stop the heart's action and the resulting cerebral anæmia, as well as the loss of consciousness, will be found to be the consequence of an impression which, from the brain, has reached the heart, and then secondarily affected the brain.

By their exaggeration, these effects are suitable for symbolizing the relations existing between the circulatory system and the nervous system, of which the heart on the one hand and the brain on the other represent the most differentiated parts. The action of the brain on the circulation is not in fact a direct one, but is executed by the intermediation of an order, or even a particular system of nerves, the vasomotor nerves. Further, this action is not limited to the heart, but is propagated to the arteries, which have a special and distinct innervation almost independent of that of the heart.

By their contraction, the arteries of the brain regulate the quantity of blood which passes through this organ, and this contraction is in its turn governed by nerves emanating from centres subjacent to the brain, which adapt its impressions to the regulation of its own circulation.

4. **Vaso-motor nerves of the brain.**—The vaso-motor nerves of the brain are contained (at least partially) in the cervical cord of the great sympathetic, and arise, as do those of the face, from the superior half of the thoracic region of the spinal cord. It is by this roundabout route that an impulse emanating from the brain, and destined for its own vessels, reaches the latter. In the brain, as in other organs, the circulation (delivery of blood) is proportionate to the activity of the function. Regulative mechanisms are provided to ensure this proportionality. These are formed by reflex cycles, whose centres of reflexion are found in other places than the brain itself, in the medulla oblongata, or in the spinal cord.

The arteries of the brain are in no sense independent of the action of the vaso-motor system, though some have declared the contrary to be the case. Their muscular elements receive nervous plexiform threads, anatomically (Bourgery) and histologically (Obersteiner) demonstrable. The very first experiments performed on the cervical sympathetic demonstrated the fact that section and stimulation of this nervous cord reverberate on the circulation of the brain.

The application of vaso-myographic methods to this circulation has again demonstrated to E. Cavazzani the reality of this influence. According to this author, *the cervical sympathetic contains vaso-constrictor and vaso-dilator elements for the brain* (as well as for the face and the retina). The first react most powerfully to electrical stimulation, their excitability is soon extinguished. The second react still more vigorously under the influence of anæmia.

Stimulation of the cervical sympathetic in man.—Jonesco and Floresco have stimulated the cervical sympathetic in man under circumstances permitting the estimation of the cerebral circulation. Its diminution is produced by feeble stimuli, leading to a contraction of the vessels ; its augmentation by strong stimuli, tending to their dilatation. This is a proof of the existence in the cervical sympathetic of elements, the one constrictor and the other dilator, destined for the brain precisely as they exist in it for other organs.

Hypophysis.—The hypophysis cerebri, or *pituitary gland*, is an organ whose functions, though still very obscure, resemble those of the thyroid and parathyroid glands, these having general nutrition and also that of the nervous system

itself under their control. These functions will be examined in their appropriate place among the secretions. The anatomical connexion of this organ, of which the larger part is glandular, with the brain is explained by comparative anatomy. In the Ammocetus, the neural cavity (which represents the ependymal canal with its ventricles) communicates with the mouth by a *bucco-ventricular canal*, and, at its other extremity, with the intestine by *a neuroenteric canal*. A circulation of water is maintained in this aquiferous system, thanks to the movements of the vibratile cilia of its wall at the entrance. Around the bucco-ventricular canal is the pituitary body, formed of epithelial cells of epiblastic origin and also of nervous elements constituting a sort of centre or special system. The aquiferous circulation which goes on in the neural canal ensures the nutrition and the oxygenation of the nervous system in these animals deprived of blood-circulatory apparatus. The secretory product cast out by the pituitary at the entrance of this current is carried away by it, reabsorbed, and thus fulfils its unknown function.

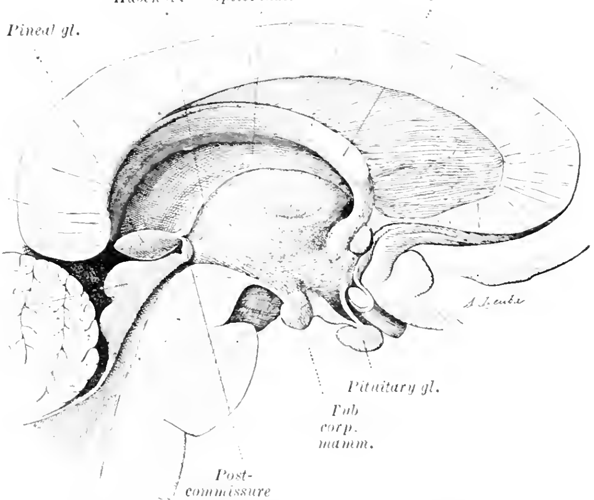


FIG. 200.—Hypophysis (pituitary gland) and epiphysis (pineal gland) (after Charpy).

When, in the course of phylogenetic development, the vessels make their appearance it is the blood which distributes both the oxygen and the secretory product ; the canal is then closed and the ventricles are shut. The thyroids are also glands annexed to the respiratory apparatus, and their method of acting on assimilation seems to resemble that of the pituitary body.

Epiphysis.—The epiphysis cerebri, or *pineal body*, is also an organ on the retrograde path. It is considered to have once belonged to the sense of sight. In phylogenetic development it represents, in certain inferior vertebrates, a single median eye, which opened outside by the parietal orifice, still existing, especially in the Saurians. The new and indeed very much less important functions of the epiphysis in superior vertebrates are practically unknown ; they are nevertheless classed with those which ensure the nutrition of the nervous system.

D. CEREBRAL LOCALIZATION

Flourens has submitted the nervous system to an analysis which has enabled him to distinguish the different functions of its most obvious

segments. According to him, *execution* of movements appertains to the spinal cord, their *co-ordination* to the cerebellum, their *voluntary* initiation to the brain : this is the first *localization* of the functions of this great system. His methods, very correct fundamentally, but insufficient in detail, led him to regard the brain, on the contrary, as a *homogeneous* mass refractory to analysis. New methods, more appropriate to the end in view, have in their turn dissociated the internal parts of this organ, as the preceding ones had separated it from specifically different homologous systems. This logical march of analysis was necessary in order that it might bear fruit. Its slowness is sufficiently explained by the difficulties of all kinds inherent in the subject, by the various questions to which it gives rise, and by the opposition with which all newly ascertained facts, with which the mind has not had time to familiarize itself, are at first met.

The method of Flourens consisted essentially in the systematic removal of parts whose functions he wished to determine. The method of stimulation was not unknown to him, but it was at that time practised in a rough manner, as, for instance, by plunging a stylet into the brain through the skull. Electrical stimulation under the ordinary form of alternating induced currents, is of recent employment ; and for nervous structures, such as the brain, it is the only efficacious method. The continuous current, very inferior to the preceding one, can nevertheless be employed to produce this stimulation.

1. Localization in consciousness

As might have been predicted, it is in the conscious life that the first phenomena furnishing evidence of functional localizations in the brain have been recognized.

1. Initial fact.—Hitzig, having noticed that in man galvanic currents applied to the posterior region of the head, or to the temporal region, produced movements of the eyes, made use of this method in order to study methodically with Fritsch the effects of stimulation of the cerebral cortex in animals, and particularly in the dog. These authors have found that *a portion of the brain's cortex is motor* (which is usually interpreted by saying that it is *excitable*), *while the other parts are not motor*. To put it otherwise, stimulation of a portion of the convexity of the brain gives rise to movements of different parts of the body, movements whose nature and genesis are disputable, but which are no longer produced when the position of the exciting agent is shifted to the outside of a fairly well defined area of which the position and limits are, apart from certain variations, constant. *These movements* take place in the part of the body opposite the stimulation : they *are*

crossed, and are also *localized* in some determinate region, as the upper or lower limb, or the eyes, varying according to the point stimulated in the cortex. The area called motor is thus itself subdivisible into smaller, partial areas. These movements are combined muscular contractions, producing a change of position in a definite direction; they have an *intentional character*. According to the point stimulated in the area corresponding to a limb, the movements of this limb will be either those of flexion, extension, or some other regular alteration of position.

These facts were confirmed by Ferrier in England and Carville and Duret in France, in the case of the donkey, the monkey, the dog, and different animals; Arloing studied them in the solipedia; François-Franck and Pitres made on this subject a very circumstantial and critical investigation. Luciani, Sepelli and Tamburini in Italy also gave them a new extension. As regards the essential facts, they were agreed; discord commenced when the question of their interpretation arose.

Method of stimulation.—Excitation is effected by means of alternating induced currents with a rhythm of about ten to the second. Stimulation brought to bear on ganglionic organs like the brain (or on the nerves which proceed to it) has effects in every way different from those obtained by directly stimulating the motor nerves. In these latter the response follows faithfully each elementary stimulation, and assumes the rhythm of the component stimulus. In the first-named, excitation only acts effectually when it is *repeated*, that is to say renewed. Further, the response no longer copies the excitation, but takes a particular form, which depends on the organization of the nervous complexus stimulated. The brain, in order to give rise to the same motor response, can therefore accommodate itself to a sufficiently varied range of rhythms. Nevertheless, the rhythm of the excitation is never quite indifferent to it. According to Richet and Broca, the stimulating effect of each induction shock should be followed (as in the heart's ganglia), by a *refractory phase*, which diminishes the useful effect of the following shock, should it arrive before the end of this phase. For the excitation of a brain in a determined condition, there must therefore be an *optimum* rhythm which should be sought for. This rhythm may vary according to the individual (de Varigny).

Mechanical stimuli are usually inefficacious, except when the cerebral excitability is augmented by a slight degree of inflammation.

2. **Discord in the interpretation.**—This discord may be explained by the very novelty of the facts to which the attention was directed. The tendency (after all a natural one) was, as is usual in such cases, to connect them with facts already known. The movements initiated by excitation in animals are of two kinds; they arise, to put it more clearly, under two very different, and in certain respects opposite, circumstances. The first are produced by stimulations directed to the muscles, or to the *terminal* portions of the nervous system, which end in the muscles; these have a purely *physical* aspect. The second

are produced by excitations brought to bear on the organs of the senses, or on the *initial* portions of the nervous system, which are connected with them ; they give rise to sensory phenomena, of which these movements are obviously the interpretation ; they bear witness to the existence of a *psychical* fact. The *intermediate* portion, the brain, the cortex, was considered incapable of excitation ; consequently the question to be solved was not as to which of the two preceding classes the movements which might arise from its being placed in a condition of direct activity belonged. Rather the novelty consisted in the fact that the excitation of this part should produce movements at all.

For their better characterization an effort has been made (by some at least) to identify them with one or the other of the two known categories. For some they were the revelation of a purely motor phenomenon, as if the stimulus in its propagation to the muscles traversed a homogeneous area, having its origin in the cerebral cortex (Ferrier). For others, they possessed the character of a purely sensory phenomenon, as if the direct excitation of the cortex only reproduced, under a new form, the indirect excitation that the centripetal nerves carried to it from the skin, across a homogeneous sensory field. This excitation would be equally reflected in some special motor centre situated lower down (Schiff).

The original interpretation given by Fritsch and Hitzig was, it must be confessed, less exclusive. The excitable areas whose existence they had discovered on the surface of the brain, and which they called centres, were denominated by them *psycho-motor centres*. Motor, they certainly were, since movement resulted from their stimulation ; in their eyes they were psychical also, because these movements possessed that character of association, combination, and adaptation by means of which we recognize the psychical nature of a motor manifestation. To make their conception more precise, they maintained that it is in these centres that the faculty of *representation of the movements of corresponding limbs* resides ; this representation having its source in the indications of the muscular sense given by the nerves which, from the muscles, ascend to the brain, and no doubt end in these centres. It is therefore in *an association of sensibility and motricity* that these authors have at first sought the explanation of the facts discovered by them, an association limited to a certain modality of sensation and of movement, but which ulterior observations and experiments will tend to extend to the tactile sense in its entirety.

3. **Number and situation of the areas capable of excitation.**—Fritsch and Hitzig (1870), in their experiments on the dog, have recognized a centre for the muscles of the *neck ;* a centre for the extensors and

adductors of the *anterior limb*; further, centres for the flexion and rotation of this limb; a centre for movements of the *posterior limb*, and one for those of the *face*.

a. *Dog*.—According to these authors, the centre of the muscles of the neck (Δ) is situated in the lateral portion of the pre-frontal gyrus, at the point where this convolution abruptly descends. The centre for the extensors and adductors of the anterior limb (+) is at the external extremity of the post-frontal gyrus, in the neighbourhood of the lateral extremity of the frontal fissure. A little behind this same fissure, and nearer to the coronal fissure, are the centres for the flexion and the rotation of this limb (+). The centre for the posterior limb (♯) is also found in the post-frontal gyrus, but nearer to the median line than is that of the anterior limb, and a little farther back. The centre for the facial muscles (○) is in the middle portion of the super-sylvian gyrus.

The results betray some inconsistency in all that concerns the movements of the neck, and, further, contractions of the back, of the tail, of the abdomen of an inconstant nature were obtained by stimulating the regions intermediate to those mentioned above, but these movements did not present the same fixity as the preceding ones. On the other hand, the whole of the convexity situated behind the facial centre appeared to these authors to be quite irresponsive to excitation, even when much stronger currents were made use of. (Hitzig, *Untersuchungen über das Gehirn*, Berlin, 1874.)

Extension of the excitable area.—Ferrier, when recommencing his experiments on localized stimulation of the cerebral cortex, repeated them on the dog, and at the same time on other carnivora, and on animals situated either higher or lower in the series (monkey, cat, guinea-pig, rat, pigeon, frog). As regards the dog, he found that its excitable area extends posteriorly as far as the fissure of Sylvius, with a tendency to go beyond it. The number of these centres, that is to say of localities in the cortex whose excitation provokes co-ordinated movements of a particular kind, is increased. This author defines the areas by numbers, and these he makes to correspond in the monkey and the carnivora. Some of these numbers are wanting in these latter, when compared with the monkey, whose brain is more differentiated.

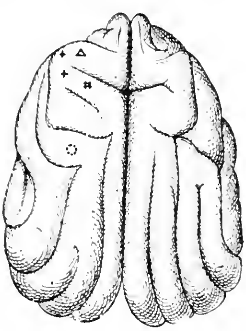


Fig. 201.—Brain of the dog, showing the psycho-motor centres determined by the researches of Fritsch and Hitzig.

Δ, movements of the muscles of the neck; +, extension and adduction of the fore limb; +, flexion and rotation of the fore limb (behind the preceding); ♯ movements of the posterior limb; O, movements of the face.

Motor centres and sensory centres.—Ferrier does not regard all these centres as being motor, even in the restricted sense which Hitzig attributes to this word. The simple fact, says he, that movements result from the stimulation of a given part of the hemisphere does not necessarily imply that this part is a motor centre, as commonly understood.

According to him, there are certain motor responses to the stimulation which express the sensation, and the character of these movements would thus form an important index to the nature of the sensation. Thus we find that, at the very beginning of all research, the question arises, embarrassing to all those who have worked on this subject : namely, by what characteristics shall we recognize motricity and by what sensibility ? And if these two conditions are distinct, where are motricity and sensibility situated ?

According to Ferrier, the criterion seems, above all, to lie in the degree of complication, association, and co-ordination, and it might be said of purpose, in the movements provoked. The more simple movements would indicate motor centres ; but if these simple movements are associated amongst themselves, as, for example, the movement of the eyes and of the head in the same direction, and, still more, that of the head, the eyes and the ears in a combined attitude expressive of attention, it must be that the stimulus has brought a sensory centre into play. The complication of the question is completed by the fact that stimulation of the same point of the cortex, according to the persistence of the excitant, or the actual value of the excitability, may produce effects which are sometimes simple and sometimes complex. The movements of the axes of the eyes may be produced alone, or may be accompanied or followed by those of the head and the ears.

Relative characters.—As a matter of fact, when we make observations outside ourselves, that is to say, external to our own proper consciousness, sensation and motion are distinguished the one from the other by characters which are not absolute, but relative. It is by relation the one to the other that two nervous elements, two systems or two centres, placed in succession, are the one motor and the other sensory, and the objective difference between the one and the other (which is made obvious by the comparison of their excitation) is never greater than when the excitation is directed to the parts between which a larger number of neurons, of systems, or of transforming centres are interposed (example : comparative excitation of the posterior and anterior roots) ; and this difference is never smaller than when these parts follow each other in immediate succession (example : the cortex of the brain).

Artificial stimulation and normal activity.—On the other hand, it must not be forgotten, that the manner in which the stimulus is made to penetrate the nervous system, in dealing with the brain, is, taking it altogether, very artificial, and does not necessarily resemble that which arises apparently spontaneously in this organ in the course of psychical activity. For the purpose of analysis we limit the stimula-

tion to a point of the cortex as circumscribed as possible, and this is roused into a state of activity by the electric current. From this point the stimulus is propagated by radiation, assuredly not of a physical nature (this cause of error may be eliminated by suitably graduating the intensity of the current) but physiological, that is to say, by reaction of the excitation by means of the elements directly excited on those in regular connexion with them. That which results most clearly from the observation of these effects is the copiousness and, at the same time, the extent of these connexions, in the first instance in the brain itself, afterwards between this organ and its subjacent systems. It is also the *pre-established order* of these connexions which causes the stimulation of determinate points to be manifested by motor effects equally determinate, and variable according to these points. In spite of the fact that we cannot avoid certain causes of error, for example, the bringing simultaneously into play of elements of which some may be excitatory and others inhibitory; or again, elements, some of projection, others of association, etc., this method is especially valuable for the analysis which, by aid of it, can be made as concerns the working of the brain; in the sense that, when we observe movements normally produced resembling those which we arouse by stimulation of a point, or of a limited area, of the cortex, we may conclude that this locality, or this area, must, in a certain way, participate in the normal execution of these movements, and also in the psychic processes connected at that moment with the execution of them.

But this method, which is favourable to analysis, only enlightens us to a very small extent concerning the phenomena of sensation, which are pre-eminently of a synthetic nature. The phenomena of cerebral activity elicited by stimulation localized at a given point of the cortex may be implicated in a sensation either actual or remembered (at the present moment, or in memory), but nothing proves to us that they form the totality of this sensation. Nothing tends to prove that this sensation or this memory, when they are the starting point for motor acts, even if resembling those produced by the localized excitation of the cortex. have for their origin a state of activity of an area also restricted to this, from whence the others are invaded by it. In fact, we know that the actual sensation (the one arising from a stimulation applied at the periphery of the nervous system) requires for its development a certain extent of the sensory area and of the cortex; at least this seems to be the conclusion to be drawn from the dispersion impressed upon it by the paths it is obliged to follow after leaving the spinal cord. In any case, in all that concerns sensation, it is necessary to be very careful in the interpretation given to the effects of stimulation

of the brain, and also in the comparisons we may be tempted to draw between it and the normal processes of cerebral activity. This much may be conceded to Ferrier, that the more a motor act permits of associated systems, so much the greater probability is there of its being accompanied by a psychism of an exalted nature, and also perhaps by a conscious sensation. But the difference is not absolute, it is only a question of degree.

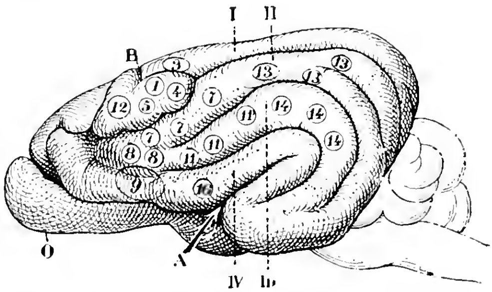


Fig. 202.—Brain of the dog (left hemisphere). Motor or sensori-motor centres, according to the nomenclature of D. Ferrier.

A, fissure of Sylvius; B. crucial furrow; O, olfactory bulb; I, II, III, IV, 1st, 2nd, 3rd, 4th convolution of Ferrier, who reckons them starting from the interhemispherical fissure; 1, 4, 5, etc., numbers of the excitable points of the cortex, whose motor effects are described in the text.

Now that these reservations have been made, we may describe the objective effects (definite movements) which are produced in response to excitations of different points of the cortex according to the numbers of Ferrier. These numbers being represented in their respective positions on a plan of the external surface of the dog's brain, in order to ascertain the area of each it is only necessary to look back to the description of the convolutions of the brain in carnivora.

(1) The opposite hind paw advanced for walking.

(3) Undulatory or lateral movements of the tail.

(4) Retraction and adduction of the opposite anterior limb.

(5) Elevation of the shoulder and forward extension of the opposite anterior limb.

(6) Occasionally, but not always, flexion of the paw accompanying movements (4) and (5).

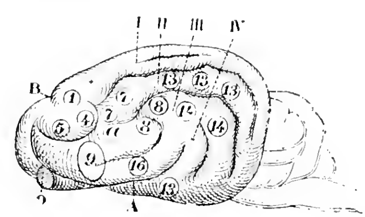


Fig. 203.—Brain of the cat (left hemisphere) (after Ferrier).

A, fissure of Sylvius; B, crucial sulcus; O, cut olfactory tract; I, II, III, IV, the external convolutions, reckoned starting from the interhemispherical fissure, 1, 4, 5, etc., numbers of the excitable points of the cortex, each corresponding to a determinate motor effect, he same for each number in different animals.

(7) Simultaneous action of the orbicularis oculi and of the zygomatici causing the opposite eye to close.

(8) Retraction and elevation of the opposite angle of the mouth with partial opening of the latter.

(9) The mouth is opened and the tongue moves.

(10) Retraction of the angle of the mouth.

(11) Elevation of the angle of the mouth and of the side of the face in order to shut the eye.

(12) Opening of the eyes with dilatation of the pupils, the eyes, and afterwards the head, turning to the opposite side.

(13) The eyes are turned to the opposite side.

(14) The opposite ear is suddenly raised or retracted.

(15) The nostril of the same side is twisted.

(16) Sometimes elevation of the lip and dilatation of the nostril ; but perhaps stimulation of the olfactory tract, which would produce these movements by reflex action.

b. *Rabbit.*—The rabbit, the guinea-pig, and the rat are lissencephalic ; this makes the mapping out of excitable points a difficult task, but a diagram will make it clear.

(1) The opposite posterior limb is advanced (when it is previously extended).

(4) Retraction with adduction of the opposite anterior limb.

(5) Elevation of the shoulder and extension forward of the anterior limb.

(7) Retraction and elevation of the angle of the mouth.

(8) Closing of the opposite eye.

(9) Opening of the mouth with movements of the tongue.

(13) Usually, forward movement of the opposite eye, and sometimes rotation of the head from the opposite side.

(14) Sudden retraction and elevation or erection of the opposite ear.

(15) Torsion or closing of the nostril.

c. *Guinea pig.*

(1) The hind paw is advanced.

(5) The front paw is raised as for walking, then it is rapidly drawn back and brought near the trunk.

(7) Retraction and elevation of the angle of the mouth.

(8) Closing of the eye and raising of the cheek.

(9) Opening of the mouth.

(14) The opposite ear is erected.

d. *Rat.*—The results are very similar to those obtained in the guinea-pig and the rabbit.

e. *Pigeon.*—The only constant motor reaction obtained by stimulating the brain of the pigeon (in the superior parietal region) is a strong contraction of the opposite pupil, associated from time to time with a rotation of the head in the opposite direction. Occasionally these two effects could be dissociated.

f. *Frog.*—Movements were noticed in the limb opposite to the hemisphere stimulated ; except their crossed action, nothing could be clearly recognized.

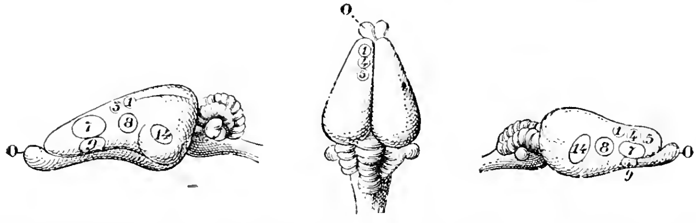


FIG. 204.—On the left, brain of guinea-pig (left hemisphere). In the middle, brain of rat (superior surface). On the right, brain of rat (right hemisphere) ; O, olfactory lobe.

1, the hind paw is advanced ; the fore paw raised ; 7, retraction and elevation of the angle of the mouth (mastication) ; 8, closure of the eye and elevation of the cheek ; 9, opening of the mouth ; 14, the opposite ear is pricked up (after Ferrier).

g. *Fish.*—The irritation of one hemisphere caused the tail to beat from the opposite side, while the pectoral, dorsal and anal fins were agitated ; the movements were complex and irregular.

The determination of the excitable points of the cortex has been carried out in great detail on the monkey, not only by Ferrier, but by many physiologists after him, especially in England. The results will

be brought forward with respect to specific innervations when the tactile cortical zone is discussed. Their interest lies chiefly in the comparison which may be made with those furnished by the anatomo-clinical method, and even with the stimulation which has been sometimes brought to bear on the human cortex.

4. **Localized ablations.**—The localized stimulation of the psycho-motor areas enables these at once to be easily recognized. Localized removal of these areas confirms the indications given by stimulation, by causing *paralyses*, also *localized* and of a special order, to appear, these being the counterpart of the preceding facts. But the location of the centres is not sufficiently fixed, nor are their boundaries sufficiently distinct, for it to be possible (after trephining the skull and laying bare the cortex) to find them to a certainty. Were it not for the indication yielded by stimulation, the search for these centres would be so uncertain and laborious, that it is easy to understand that this method, as formerly practised, would never have led to their discovery. But *if, the location of a centre having been ascertained by excitation, the cortex corresponding to it be removed, paralytic phenomena will make their appearance in precisely the same region as that of which the excitation of the centre caused the movements.*

The functional deficiency following this ablation is not a paralysis, if by this word is understood the total loss of movement in the corresponding limb. The limb is not deprived of all movement, but it is deprived of one of the determining conditions which engender this movement in it. It has retained reflex and automatic movements, even a part of its instinctive movements ; on the other hand, it has lost those movements which are called *voluntary*, and especially those which a more or less long and patient education had *acquired* for it. The animal can make use of its limb for walking or jumping, but it will no longer be able to use it for holding the bone it wishes to gnaw, or "to give a paw," as it has been taught to do at the word of command.

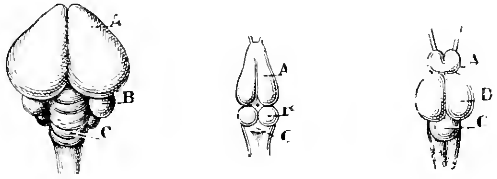


Fig. 205.—On the left, pigeon's brain. In the middle, frog's brain. On the right, carp's brain.

A, cerebral hemispheres; B, optic lobes; C, cerebellum; X, location of an excitable point in the pigeon's brain (after Ferrier).

5. **Disturbances of sensation.**—The disturbances of sensation which follow a limited destruction of the cortex are no less characteristic than those of movement. All sensation has not vanished from the limb which we describe as paralysed. The animal reacts to stimuli

applied to the skin of this limb, but it is a kind of sensation that is at first sight seriously altered. Sensation, the conscious representation of the *attitudes* of the limbs, is lost. The animal often walks on the dorsal surface of its toes without appearing conscious of doing so. In repose, in the upright position, it often falls on the side of the limb attacked by these disturbances of sensation and movement; it can, it is true, get up again by itself. When lying down, it endures the most uncomfortable positions, without trying to alter them.

When, in the cortex, we remove that which is called the "centre" appertaining to a limb, or to any segment of the body, we obviously destroy an association between sensation and movement. The data yielded by experiment agree on this point with those furnished by anatomy, which shows us the sensory and motor tracts mutually connected in a certain manner in this cortex.

The corresponding limb has not lost all power of movement, for it is seen that it can execute many and even complicated acts; it has not entirely lost sensation, inasmuch as it reacts to painful and even tactile impressions. This is because the sensory nerves of the limb form other connexions with its motor nerves, either in certain areas of the cortex different from the first, or especially in the grey subjacent masses, and each of these associations answers to some special function. Of these functions, the one which is exerted in the area of the excitable zone corresponding to a given limb has for chief object the solidarization of motion and sensation in this limb, for the performance of certain conscious-voluntary acts.

Nevertheless, it is not only that which is usually called the muscular sense which is in this case disturbed or destroyed. If, as Tonnini has remarked, the alterations of this sense are graver and persist longer, *yet all varieties of sensation are in reality involved*. The special tactile sense is itself diminished, and the contact of bodies is only perceived after a considerable interval, this delay being due to retardation undergone by the transmission and elaboration of the sensation (R. Tripier). Sensibility to pain is also diminished, as are also the tactile sense and the cœnesthetic sensations (Verger).

6. **Comparison of motor and sensory disturbances.**—Compared with motor disturbances, those of sensation are *more diffused*, and sometimes reach, but imperfectly, areas (a limb for example) other than those in which the motor paralysis is localized. They are, on the other hand, *more fugitive*, and in about a couple of weeks begin to diminish and then soon disappear. In the order of sensation, as in that of movement, but especially in that of sensation, these disturbances are the more recognizable and durable according to whether or not a more

differentiated function is in question. More marked in the foot, and, above all, in the hand, than in other regions, they are so also in superior species, rather than in the inferior animals (Mott).

7. **Evolution of this question.**—The question of cerebral localization has been brought to the front by the discovery of an excitable area on the surface of the brain. For a short time it seemed necessary to copy its first expression from that which portrays the functions of the nerve roots by simultaneously distinguishing between the nerves of sensation and those of movement in them. But facts soon showed that one of the most essential functions of the brain is, on the contrary, to solidarize sensation and motion, to efface between them those characteristics which, without being absolute, make them appear so different when we examine them at the periphery of the nervous system; and to effect the transition, though in the main unknown, which leads from one to the other.

The actual formula of this discovery is founded on a distinction of another order. Sensation is no longer separated from movement; the *different modalities of sensation* are separated instead, at the same time attaching to each of them the equally different modalities of that variety of motion which is the most nearly related to them. In this way a certain number of *specifically different systems* are constituted, each one answering to the exercise of one of our senses. On the other hand, it must not be forgotten that these systems are connected the one with the other, and are also capable of resolution into their constituent elements, and that by this double means they may produce the most different combinations.

8. **The tactile system.**—The area known as the excitable area of the brain defines, on its surface, the locality occupied by general sensation or the tactile sense. The muscles of the limbs, of the face, and of the trunk, which are in immediate anatomical and functional connexion with the skin, this being the receptive organ of tactile excitations, are naturally attached to it by reflex arcs whose circuit is completed in the spinal cord, the optic thalamus and the cerebral cortex. Thus arises a natural system of the highest importance, namely: the tactile system, which, answering to a modality of sensation common to all our organs, extends its roots to the immense majority amongst them, reserving at the periphery some very restricted areas, for the reception of stimuli corresponding to the other senses.

Alongside this system are placed others, constructed on the same type, but at the same time specifically different both as regards the nature of the stimuli which bring them into play, the sensations arising within and the movements directly at the service of these sensations.

These systems are represented in the cerebral cortex, of which they occupy certain areas, areas whose outlines, it is true, are not very clearly defined, but which are nevertheless perfectly distinct, and whose extent cannot be measured by that of their peripheral area alone, but rather by the importance of the information furnished by them to the sensorium.

The delineation of these areas is the precise problem of cerebral localization, such as it exists at the present moment. The methods made use of for resolving the question are, on the other hand, those which have served for the cortical area subserving general sensation. They consist of localized and methodical destructions of the cortex and of its stimulation. These localized destructions are followed by *sensorial paralyses* of a nature specifically different, according to the function of the area destroyed. As to the *excitations*, they produce movements which are in functional relation to the stimulated area. Clinical experience has also furnished a valuable quota of observations.

9. **The sensorial systems.**—By means of information drawn from these different sources, it may be concluded that the brain is composed of different parts, of differentiated systematizations, whose principal modalities correspond with the five different senses into which our sensibility is divided. The posterior part of the brain, its *occipital* pole, is devoted to *vision*. A part of the *temporal* region (first and second temporal convolutions) is given over to *hearing*. The *limbic* convolution (the whole of it in osmatics, the hippocampal lobe in microsmatics) is appropriated to *olfaction*. The seat of taste is less certain, but is probably situated in the neighbourhood of the preceding area, if not included in it.

By the localized destruction of one of these areas of the cortex to the exclusion of the others, an individual may therefore be deprived of a determinate order of sensations, while retaining the remainder. For example : sensibility to light may disappear (psychical blindness) while the other modes of sensibility (tactile, auditory, etc.) are preserved. It seems as if plain facts like these can allow of no further hesitation as regards the still disputed question of cerebral localization.

Localization, differentiation.—In truth, these controversies concern less the reality of the facts than the suitability of the expressions employed. The words " centres " and " localizations " in particular, if taken literally, can only serve to perpetuate these discussions. An injury localized in a given area of the brain (or of the nervous system) produces a definite perturbation of the functions of the brain (or of the nervous system) ; this is brought out clearly from the facts of observation and experiment, and definitely undermines the former hypothesis of the homogeneity of the brain's functions. But if it be argued from this that the vanished function is localized in the area of the brain which has been destroyed, the conclusion transgresses the limits of fact, as it is clear that the function whose

disappearance is under observation requires the co-operation, not only of an area of the cortex, but also of the connecting links attaching this to the subjacent regions of the nervous system, or even to the neighbouring regions of the cortex itself. And if it is said that this function is centralized here, the expression is not much more accurate; because, in spite of the preponderating part which the cortex plays in the connexion between the elementary acts co-operating in this function, it does not exclude the part played by other associations which are produced outside the cortex in masses of the grey matter; these possessing the same structure as the cortex, but in a simplified condition. In the present state of our knowledge it would be more correct to say that the brain (like the whole of the nervous system) is composed of *differentiated systems*. These systems are constructed on a uniform type (cyclic systems), and can be brought into action only by the agreement of their component parts: but, being repeated either in a parallel or successive manner, they adapt themselves to different functions which answer either to a variety of modalities, or to the elaboration of their primordial function.

In one direction as in another, this differentiation is not uneven but progressive. The most correct formula would therefore be the one which, while insisting on this differentiation, would at the same time take into account its transitions and its gradations.

Opposition of the points of view.—With regard to the cerebral localizations, Goltz and Munck, while fundamentally insisting on the same facts generally held as correct, have supported two almost antagonistic points of view. Goltz removed the cerebral cortex from a dog (with the exception of certain portions in the neighbourhood of the optic nerve and the olfactory lobe). When the animal had recovered, he endeavoured to ascertain in what the functional deficiency following such an operation consisted. He found that the animal had retained some sensations, notably that it could see, hear and smell; he even recognized in it some lingering traces of instinct. Munck, both from his own experiments and from the criticism to which he subjected the observations of Goltz, could see, in the functional manifestations of this dog deprived of the cerebral cortex, only very complicated reflex movements, without any trace of consciousness.

Differences of the criteria.—The following is the criterion of Goltz. In living beings other than ourselves, we recognize the existence of conscious phenomena only by the motor manifestations to which they give rise; and we recognize these only on the condition that they are a logical answer to the stimuli applied by us to these beings. If an animal cries out when it is hurt, it is reasonable to infer that it feels. If it closes its eyes before a too brilliant light, it does so because it sees. If it takes to flight or stops its ears in the neighbourhood of a violent noise, it is because it hears. If, when placed in the presence of its food, it eats, this shows that it has still the instinct of self-preservation. If it were, however, without a cerebral cortex, or even without a brain, how much in degree it would retain of all this remains still to be determined.

The criterion of Munck is quite different. This author lays down as a principle the fact that there is nothing in common between the movements called reflex and those which have for starting point the internal phenomena of the consciousness. It is known, says he, that an animal with the spinal cord cut (but not destroyed) is sometimes capable of performing complicated reflex movements in response to stimuli applied to it. These so-called conscious manifestations of Goltz's decerebrated dog are only much more complicated reflex actions, which may be compared to those of the spinal cord. The cerebral cortex is alone the seat of conscious actions. The author does not take into consideration that it is possible to reverse his reasoning, and by degrading consciousness in

exactly the same degree as that to which he raises reflex action, to attribute it to the spinal cord. Nevertheless, of the two points of view this would be the more scientific; it has the law of continuity on its side, while the other, arguing from certain incontestably great differences between cerebral and medullary manifestations, places them in what may be considered as an absolute opposition.

In short, it is necessary to distinguish between a *crude* and an *elaborated* sensation. The first is located in the sub-cortical centres, and becomes the second by attaining perfection in the cerebral cortex. This doctrine was the one adopted by Longet, who confirmed it by observing that a pigeon whose brain had been removed could still follow with its eyes a light moved about in front of it. On the other hand, we may also admit that, in the animals most elevated in the series, the cortex plays a predominating part: while in inferior vertebrata it leaves a larger share to the activity of the inferior centres. Richet has observed that if, in the pigeon, the cortex alone is removed (instead of the whole brain) the resulting deficiency amounts to very little. Of these two sensations, the one of a crude nature and the other elaborated, the first by its very imperfection eludes consciousness; it is only made known to us by becoming the second, that is to say, an elaborated sensation, and in this case merely plays the part of an indissociable element. It is therefore necessarily unknown to us except by reasoning.

2. Localizations in unconsciousness

The motor effect of stimulation of the cerebral cortex is not limited to the contractions of the muscles of the skeleton. This stimulation reacts equally on the movements of the *circulation* (heart and vessels), on those of the *intestine* (in its whole length), on those of the *glandular* reservoirs (urinary bladder), as well as on the *secretory* organs themselves. In brief, it may be said that no organ escapes the cerebral influence. This fact, the action of the brain on the nutritive function, was at first received with surprise and misgiving, because it disagreed with the far too simple idea which had for a long time prevailed concerning the distribution of the functions between the two great divisions of the nervous system.

To the first of these (cerebro-spinal system), of which the brain was an essential part, were assigned conscious voluntary acts: to the second (great sympathetic system) the unconscious involuntary phenomena were relegated.

It had already been demonstrated that the second of these systems (great sympathetic) was prolonged into the former, by seeking its origins in the spinal cord; it had even been followed higher still into the medulla oblongata, where important centres had been found belonging to it. But however high it might ascend, no one ever even imagined the possibility of its reaching the cerebral cortex, this being reserved by definition for conscious acts, from which the great sympathetic system is excluded. As a matter of fact, the division between the two is not such a simple one, and, above all, is not made according to a plan sketched out below the cortex or at some distance from it. A large number of facts go to prove that functional acts attain their highest perfection of consciousness only when the cerebral cortex participates in their execution. But we cannot admit that this participation of the cortex necessarily implies a conscious character as concerns every act in which it co-operates, as there are so many examples to prove the contrary. Further, that consciousness may in no degree

exist apart from the co-operation of the cortex is less and less admitted, transition and gradation between consciousness and unconsciousness seeming more probable than absolute contrast and opposition between these two conditions.

The influence of the cerebral cortex on unconscious movements is undeniable. The difficulty that lies before us is to know to what circumstance, or to what kind of organization, is due the fact of this influence being of a different nature from that exercised by the cortex on the muscles of the life of relation. A parallel between the two systems, one of animal and the other of vegetative life is easy enough to draw in all that relates to the two sub-systems or inferior arcs which serve them as a basis, and this parallelism may indeed be extended to a certain distance in the spinal cord, but no fixed data exist with regard to what concerns the superior portions of both these systems.

A. Respiration.—The movements of the thorax and the diaphragm correspond to several functions, of which two of the principal are : *pulmonary ventilation, and the emission of sounds.* In the spinal cord, in the medulla oblongata, in the basal ganglia, and, finally, in the cortex itself, the associations governing these two kinds of movements are effected. Let us consider principally respiration.

The *medullary centres* when left to themselves have only a trace of organization as concerns respiration.

The *bulbar centre* and the nuclei, both inspiratory and respiratory, contained in it, have an *essential action,* in itself sufficient to maintain the regularity of the respiratory movements.

The *cerebral ganglia* and the *cortex* have an action not absolutely necessary, but of an *efficient* nature. Emotional disturbances of the respiration have caused this to be suspected, and stimulation of the parts has demonstrated the fact.

Danilewsky, Munck, Bochefontaine, François-Franck, Bechterew and Ostankow, Spencer and Horsley have observed accelerations, slackenings, and stoppages of respiration caused by localized stimulation of the cerebral cortex. These centres, and especially that of inhibition, are situated in the antero-external part of the second and third convolutions.

It is possible to follow the conducting fibres starting from this area in the corona radiata where the impulse will find them again and will give rise to the same effects. They usually pass through the knee of the internal capsule.

Movements of the larynx.—These are of two kinds, corresponding to the two essential functions of the larynx, *respiration* and *phonation.* They both employ most of the muscles of the larynx, but in an unequal manner. The first consist essentially in an *abduction* of the vocal cords, which causes the opening of the glottis at each movement of inspiration ; the second in an *adduction* of these parts, with contraction of the orifice of the glottis. For both of these movements two parallel

innervations may be found, and these may be followed up to the cortex. But for the respiratory movements the action of the medulla oblongata is essential, because these are above all of a reflex order and represent a function which is always being exercised ; for the movements of phonation, the cortex is the *primum movens*. These centres are bilateral, that is to say, they govern two sides of the larynx (at least in animals).

If the before mentioned areas of the brain's surface (*gyrus precrucialis*) have been laid bare, and if the movements of the glottis are examined under stimulation of these areas, the latter will be seen to open during movements of inspiration. If the locality of the stimulation be changed, a region will be found in the neighbourhood (isthmus of the pre-crucial gyrus) which closes the glottis, producing at the same time acceleration of the respiration ; it should correspond to a centre of phonation.

B. Circulation.—Hitzig, Eulenbourg and Landois, Bochefontaine, Lépine, and others after them, have observed that destruction of the excitable area (sigmoid gyrus in the dog) is followed by a *paralysis*, which is not only motor, but is also *vaso-motor*, as regards the areas corresponding to the part of the cortex destroyed. This vascular paralysis is marked by an elevation of temperature, due to the exaggeration of the capillary circulation, and to the resulting loss of heat in the area which is the seat of this hyperæmia. Without being exactly superposed, the motor and vaso-motor centres of a given region (of a limb) are very close to each other, and arranged nearly in the same order. Stimulation of the cortex may cause contraction of the vessels (lower the temperature locally) to the same extent as its destruction causes the opposite effect.

Vaso-motor area.—According to Bechterew and Mislawski, the vaso-motor area of the cortex extends beyond the motor area ; it includes not only the sigmoid gyrus, but also a territory extending behind it, and encroaches even on the temporal lobe (anterior part of the second and third primitive convolution, superior part of the fourth). These authors found that stimulation of the posterior portion of the sigmoid gyrus (behind the crucial furrow) caused *vaso-constriction ;* that of certain portions of the anterior region of the sigmoid gyrus, as well as some points, both of the second and third parietal convolutions, produced *vaso-dilatation*. Their method of observation consisted in measuring and registering the general arterial pressure ; its elevation indicating a constriction, and its lowering a dilatation of the peripheral vessels.

Basal ganglia.—Bechterew and Mislawski have also observed that

stimulation of the ganglia of the base of the brain is accompanied with vaso-motor effects (constrictive), these effects being more marked when the *optic thalamus* and the *globus pallidus* are stimulated, very feeble when other parts are excited, and as feeble as it is possible for them to be when the stimulus is applied to the caudate nucleus. These effects may be reproduced by the stimulation of the internal capsule (principally its posterior segment); and they are also observed after degeneration of the pyramidal tract. Thus we ascertain the fact that the basal ganglia are united to the subjacent parts by special fibres, at the same time that they exchange impulses with the corresponding cortex.

Heart.—The same authors have observed that stimulation of the *sigmoid gyrus*, independently of its merely vascular effect, produces acceleration of the heart and a slowing of the same which is generally of a secondary nature, but may also be primary. After the removal of the cortex the heart's action may be stopped by stimulation of the *corona radiata* at a point corresponding to the anterior frontal convolution. The tract thus stimulated must enter into the construction of the cortico-thalamic radiation, as, by excitation of the external portion of the thalamus, the same effect of stoppage of the heart in diastole may be observed.

Tarchanoff recorded the case of a young man who possessed the faculty of voluntarily accelerating the beating of his heart. He was a very excitable subject. He could also move certain muscles over which the will usually has no control, such as the muscles of the external ear.

Thermo-regulative function.—Between the circulatory and the other sensori-motor functions demonstrated by these experiments, both being represented in the cerebral cortex, the relations are very numerous. The point of view from which they can be most distinctly observed, is without contradiction that of the regulation of the temperature, or, to put it better, the equilibrium between the production and the loss of heat which ensures the thermometrical constancy of the organism.

The excitable area, in so far as it is motor in function, produces heat; this same area, in so far as it is vaso-motor, preserves (vaso-constriction) or loses (cutaneous vaso-dilatation) this heat. The equilibrium which regulates this heat and keeps it at a constant level, will therefore depend on an agreement established between these component elements. An agreement like this between such different motor effects necessarily presupposes, in the living being, a sensory phenomenon naturally capable of co-ordinating them. And this phenomenon is not lacking here. It is sensibility to heat which in the same degree as the other cutaneous sensibilities, appertains to the tactile area, from the fact of its sensori-motor nature. The cortex may certainly contribute to the regulation of the temperature, and may take part in the struggle against cold which we call conscious. But this regulation may, and usually does take place without its intervention, by an unconscious process, of which the preceding associations give us merely a model in the order of consciousness. In the basal ganglia, in the medulla oblongata, even in the spinal cord itself, functional connexions arise, whose aim is the same, and of which certain have a preponderating influence.

C. Digestive functions.—The brain has an equal influence on the digestive functions, as will be seen from the following facts.

Mastication, deglutition.—By stimulating the cortex in the neighbourhood of the sigmoid gyrus, movements of the mouth, the tongue and the jaws are produced (Ferrier). But if the stimulus is brought to bear on the second convolution (that enveloping the sigmoid gyrus) in the exact prolongation of the crucial furrow, genuine *masticatory movements are produced, succeeded by deglutition* (Rethi). Thus a prearranged association is brought into play, which is controlled by this region of the cortex; this association produces the act of *mastication.* These co-ordinated movements may also be produced by stimulating the subjacent white substance. This can no longer be done when the crura cerebri below the optic thalamus are stimulated. The association, as regards its most essential factors, must lie, therefore, either in the optic thalamus or in its inferior portion. Stimulation of the posterior part of the floor of the fourth ventricle also provokes swallowing. Stimulation of the optic thalamus elicits co-ordinated movements of mastication, followed by deglutition; it also affects the movements of the stomach and of the intestine. This ganglion therefore possesses great importance in the association and the co-ordination of movements corresponding to the vegetative functions, or to those of nutrition (Bechterew).

Movements of the stomach.—The immediate centres of the organs we are now about to mention are no longer situated in the spinal cord, but in the ganglia of the great sympathetic. The stomach contains a certain number of these disseminated ganglia, which, though much more numerous, call to mind those of the heart, and which exist independently of the plexus of Auerbach. These ganglia receive the fibres of the great sympathetic (properly so called) and also of the pneumogastric and, by the aid of the nuclei of this latter contained in the spinal cord and in the bulb, they are attached to the encephalic ganglia and to the cerebral cortex. Detailed researches have been made on this question by Openkowski, Bechterew and Mislawski.

In the spinal cord the origins of the nerves of the stomach (splanchnic) extend from the fifth to the eighth thoracic pair; the fibres uniting them to the brain pass into the anterior columns. They represent an important, and indeed an essential, reinforcement of the ganglia of the base: caudate nucleus, lenticular nucleus and corpora quadrigemina; they are connected with the cortex. Special innervations for the cardiac orifice, the body of the stomach, and the pylorus must be distinguished.

Cardiac orifice.—Its centre of dilatation is at the union of the antero-inferior extremity of the caudate, and lenticular nuclei near to the

anterior commissure ; it acts, through the vagus and sympathetic nerves and their terminal ganglia, by relaxing this orifice ; this centre is united to an area of the cortex situated in the neighbourhood of the crucial furrow. The two splanchnics, large and small, which, arising from the sympathetic chain are in part distributed to the stomach, thus participate in this innervation ; the large splanchnic as a centrifugal, and the small splanchnic as a centripetal nerve, by a reflex cycle. The opening of the cardiac orifice may, however, ensue in a reflex manner by stimulation of a large number of organs, including the viscera.

Body of the stomach.—The muscles, ganglia, and nerves are less numerous here and less powerful ; the movements are also less energetic, and consist of rhythmical and peristaltic waves going from the cardiac orifice to the pylorus. These movements are governed by the vagus and the principal encephalic centre is in the corpora quadrigemina. An inhibitory action, antagonistic to the preceding, is exercised by the splanchnics, and controlled by the spinal cord. No connexion of these centres with the cortex as regards the body of the stomach has been discovered, but only for its pyloric portion, a general contraction of which, with cessation of the rhythmic movement, can be induced by stimulation of the sigmoid gyrus (Bechterew and Mislawski).

Pylorus.—In this locality the muscles are powerful and the ganglia are numerous, innervation giving rise to relatively energetic movements. The vagus and the sympathetic govern these movements by means of the splanchnics. These nerves are, in the pylorus, made up of a mixture of excitatory and inhibitory fibres, of which one or the other predominate, according to the animal.

The centre for dilatation of the cardiac orifice, either that situated in the cortex or that located in the corpus striatum, is a constrictive centre for the pylorus ; a centre of dilatation for this sphincter is, on the other hand, located in the corpora quadrigemina.

Movements of the intestine.—These have been studied by Bechterew and Mislawski ; the general outline of their work is the same as that given above. The small intestine is innervated by the sympathetic and the vagus. The first of these nerves is especially inhibitory in action, the second chiefly motor, as in the case of the stomach. The sympathetic elements leave the spinal cord from the sixth dorsal up to the first lumbar.

The large intestine is innervated by the great sympathetic, and by the erector nerves which go to the hypogastric plexus. The origins of the sympathetic elements are in the first lumbar pairs ; the erector

nerves come from the first, second and third sacral pairs. In ascending from the intestine to the cerebral cortex, we traverse the terminal plexuses (of Auerbach and of Meissner), we follow either the branches of the vagus or those of the great sympathetic (splanchnic nerve), we pass through the dorsal and cervical part of the spinal cord, and also of the bulb, and finally we find in the optic thalamus an essential centre of association, not only for the movements, but also for the secretions of the intestine.

It is for this reason that, in birds, if the optic thalami are removed at the same time as the hemispheres, all food remains in the gizzard; serious digestive disturbances ensue, and the animal finally dies of starvation. If the optic thalami are preserved life may last a very long time, provided food is given artificially. If, in mammals, the optic thalamus is uncovered, the lateral ventricle opened, and the hemispheres are removed and stimulation is brought to bear on these ganglia by the help of fine electrodes sunk in their substance, either movements of the intestine result, or relaxation of its walls and stoppage of the peristaltic contractions. Stimulation of the middle region of the thalamus rather tends to strengthen, though inconstantly, the movements of the intestine, both peristaltic and rhythmic. That of the *external* nucleus relaxes the wall of the small intestine, and arrests the peristaltic movements. That of the *antero-external* region acts on the large intestine, whose movements it stimulates up to the point of causing defecation. The proximity of these two segments makes it sometimes possible to obtain simultaneously the two effects, namely: relaxation of the small and contraction of the large intestine.

On the cortex, in the sigmoid gyrus and the posterior part of the second convolution which encloses it, areas are to be found stimulation of which induces the whole series of preceding effects, but more often those limited to certain regions of the two intestines; with these peculiarities, however, that the effects are feebler, the latent period longer, and the excitability of the grey substance much more quickly exhausted.

Sphincter of the anus.—In inferior mammals the sphincter of the anus may be caused to contract by stimulating the cortex a little behind the crucial furrow on the posterior segment of the sigmoid gyrus, near to its external border (J. Meyer). In the monkey, the *ano-cortical* centre is on the posterior portion of the paracentral lobe (Sherrington). The ganglionic reinforcement of the base of the brain corresponding to this innervation has not yet been determined, but owing to the experiments of Goltz, its medullary reinforcement, or *ano-spinal* centre is known, this being situated in the lumbar spinal cord, at the level of

the sixth and seventh vertebræ in the rabbit, and of the fifth in the dog.

The functional antagonism between the anal sphincter and the expulsive muscles of the rectum is also, in a certain degree, displayed anatomically by the provision of definite fibres which proceed to the first and second of these muscles. The law laid down above requires that the transverse fibres, those of the sphincter, should be chiefly innervated by the branches of lumbar origin, emanating from the sympathetic chain (inferior mesenteric ganglion and nerve), and that the transverse fibres of the rectum should be chiefly supplied by those arising from the sacral spinal cord. In reality there is a mixture of elements, and the hemorrhoidal or anal nerve (of sacral origin) is the constrictor of the anus.

Rhythmical contractions of the anal sphincter.—After the removal of the ano-cortical centre, rhythmical contractions of the sphincter of the anus may be observed (V. Ducceschi) which others have noticed after the removal of the spinal cord in its inferior portion (Goltz and Ewald). These contractions are difficult to explain: they may possibly be attributed to an abnormal transmission to its sphincter of the rhythmical excitations of the intestine. The anal sphincter is, however, a special muscle; although belonging to the intestine, it is made up of striated fibres. It is obedient to the will, though at the same time being an organ whose action is especially tonic and reflex. It resembles the diaphragm, which is also a voluntary and automatic muscle, and one which, like the anal sphincter, contracts rhythmically after being excised.

D. Secretions.—Bochefontaine and Lépine have observed that stimulation of the cortex applied to the sigmoid gyrus and neighbouring parts causes the *salivary glands* to secrete in a bilateral or rather a crossed manner. Bochefontaine has also observed that stimulation of the motor area in the dog influences the *biliary secretion* of the liver, and also the secretion of *pancreatic juice*, both of which secretions it diminishes. The same author has further observed *contraction of the spleen* to follow stimulation of the anterior part of the brain. At several points (1, 3, 4, 11 of D. Ferrier) Bechterew and Mislawsky have provoked the secretion of *tears*, by stimulating the cortex at the sigmoid gyrus in the interhemispherical fissure, that is to say, by bringing the stimulation to bear on the *internal part of the anterior and posterior convolutions of this gyrus*. Excitation of the convexity of the gyrus has only a very feeble action; and, apart from it, nothing is produced in this direction. The effect is bilateral, but less on the side submitted to excitation. At the same time dilatation of the pupils, accompanied by projection of the ocular globes, and shrinkage of the third eyelid may be observed; these phenomena always appearing earlier on the side opposite that stimulated.

If, once more, we leave the peripheral organs, in order to ascend to

the cortex, by following the paths of the impulse, we shall find, in the neighbourhood, or even in the substance, of the glands, ganglia of the great sympathetic; from these spring branches, either direct (visceral) or indirect (intermingled with mixed trunks) which are detached from the chain and have their origins in the spinal cord, or else branches of the cranial nerves (chorda tympani), which are the equivalents of the branches of the great sympathetic in this region. Afterwards from the bulbar or medullary centres we ascend to a ganglionic reinforcement or centre of association, this being constant for all functions of this order and having an exceptional importance in the government and the regulation of nutritive phenomena; this is the optic thalamus. From this we reach the cortex of the brain.

Lachrymal secretion.—The lachrymal secretion, in particular, displays this succession and this concatenation in a very distinct manner. It is governed, starting from the spinal cord and the bulb, by that part of the great sympathetic which, arising from the superior thoracic spinal cord, ascends along the cervical chain as far as the trigeminal nerve. Some elements come from the medulla oblongata by the trigeminal itself (strengthening origins), and all of them proceed to the gland by the lachrymal branch of the ophthalmic division. The greater or lesser part taken by one or the other origin in lachrymal innervation is the only point which gives rise to differences of opinion on this subject. The original nuclei of these bulbo-medullary nerves are attached to the optic thalamus, which forms a centre of reflexion of great importance for the lachrymal secretion. The direct stimulation of the optic thalamus at its lower and internal portion, near the grey commissure, is followed by secretion of tears on both sides (predominance of the opposite side) with dilatation of the pupils and protrusion of the eyeballs.

Stimulation of the cortex in the before-mentioned points of the gyrus has the same effect.

The lachrymal secretion thus provoked by stimulation of the optic thalamus and the cerebral cortex resembles that which accompanies certain psychical processes (emotions). Salivation is, on the other hand, a symptom of certain mental or nervous affections (Esquirol, Foderé . . .). It is also observed in epilepsy during the attacks, or in the form of crises equivalent to these attacks themselves (A. Koranyi, Ch. Feré). On this point it is necessary to notice the difference in the nature and appearance of the saliva, according to the conditions of its secretion, its glandular origin, and the locality of the excitations provoking this secretion. A similar gland, the sub-maxillary, yields either a viscous or watery saliva according to which of its two secretory nerves, the great sympathetic or the chorda tympani, is stimulated. The first is usually called "sympathetic saliva," and the second "cerebral saliva," but this is most incorrect, inasmuch as the two nerves are ganglionic and similar to each other, one coming

from the spinal cord and the other from the medulla oblongata. But pathological or artificial excitation of the brain causes (no doubt by the intervention of the great sympathetic) a viscous saliva to be secreted, and to this the name of "cerebral" would be much more appropriately applied, since the stimulation in this case would be distinctly a cerebral one.

E. Contraction of the bladder.—Bochefontaine, by stimulating the motor area, caused the *urinary bladder* to contract with partial expulsion of the urine contained in it. François-Franck has obtained similar results when recording the vesical pressure. Bechterew and Mislawsky have localized the area of the cortex, stimulation of which induces this action, in *the internal portion of the anterior and posterior segments of the sigmoid gyrus.*

The same result ensues when the optic thalamus is stimulated, the stimulus being applied to the inferior portion of the anterior nucleus. Other portions of the optic thalamus and corpus striatum do not when stimulated yield the same result. But it ensues when the posterior segment of the internal capsule in proximity to the thalamus or the tegmentum under the corpora quadrigemina is stimulated. Doubtless Budge stimulated these fibres when he found that contraction of the bladder was induced by excitation of the crura cerebri. These unite the optic thalamus to the spinal cord and, through the nuclei of the latter, the stimulation reaches the bladder by following the great sympathetic (mesenteric nerves) and the erector nerves, whose fibres are intermixed in the hypogastric plexus.

A functional antagonism exists between the muscles of the fundus of the bladder (*detrusor urinæ*) and of the sphincter of the latter. The sphincter muscle, by its tonic contraction, retains in the bladder the urine which the latter tends to expel at certain periods. The *detrusor urinæ*, or muscle expulsive of the urine, is innervated by the branches of the erector nerves. Expulsion of the urine is provoked when the *anterior* roots of the two first sacral pairs are stimulated, which contain the origins of these nerves whose morphology is special (Morat). On the other hand, the sphincter is put in action when the sympathetic branches are stimulated, which arise from the third, fourth and fifth lumbar pairs and pass through the inferior mesenteric ganglion in order to supply the mesenteric nerves, themselves terminating in the hypogastric plexus and, through it, in the bladder (Courtade and Guyon). According to J. Meyer, there is a special cerebral localization for the sphincter of the bladder. This author places it in the external portion of the posterior segment of the sigmoid gyrus.

F. Genital organs.—Bochefontaine observed contraction of the Fallopian tubes to ensue as the result of faradisation of the gyrus around the external extremity of the crucial sulcus.

Both spontaneously and after the interruption of its communications with the spinal cord, the *vagina* in the bitch is the seat of rhythmical movements which are thereby rendered more forcible by stimulation (Iastreboff). The automatic ganglia of this organ are connected with

the spinal cord by means of the ganglia of the sympathetic chain proceeding from the second lumbar to the fourth sacral. Stimulation of the communicating branches of the sacral nerves also reinforces the vaginal movements (Langley). As regards the vaso-motor phenomena, they are under the control of the nerves following the same paths, and of which some cause vaso-dilatation (third and fourth sacral), others vaso-constriction (first and second sacral). Furthermore, this system of nerves also supplies the *penis*.

The movements of the vagina are affected by stimulation of the sigmoid gyrus either in the direction of augmentation (stimulation of the posterior region), or in that of arrest (stimulation of the antero-external region), though no definite distinction exists between the areas producing these contrary results.

These effects are also produced when the anterior half of the optic thalamus is stimulated in the neighbourhood of the area which presides over the bladder and rectum. These grey masses are connected with the great sympathetic by bulbar and spinal centres, stimulation of which also acts either by inhibiting or by provoking movements, yet with certain differences in the character of these movements, which vary according to the different areas stimulated (Bechterew and Mislawsky).

Persistent influence of the brain on the spinal cord.—Sensory impressions, more especially when of a lively nature, exert on the superior centres (notably on the brain), an effect which may persist long after they themselves have disappeared. As regards motor impressions leaving the brain to proceed to the spinal cord, it is generally maintained that their effects scarcely survive their disappearance. Brown-Séquard, R. Dubois, Tissot and Contejean bring forward facts which tend to show that the spinal cord may retain something of these effects even after removal of the brain. The first of these organs, therefore, appears to possess a certain faculty for the preservation of stimuli, though much restricted in comparison with that of the second.

Examples.—A duck from which one of the two hemispheres has been removed walks obliquely on account of the paresis of the muscles of the side opposite to the lesion. If the cervical spinal cord be cut across and the animal be placed in water, it will swim, and in swimming will follow an oblique direction. The ablation of the whole of the encephalon does not have the effect of re-establishing equilibrium, a proof that the want of equilibrium has been felt by the spinal cord and is persistent after the suppression of the portion primarily injured.

If the motor area of the cortex on the left side be removed in a dog affected with St. Vitus's dance, it will be seen that the clonic attacks are augmented on the right side and preserve the same intensity on the left. If, later, the spinal cord below the medulla oblongata be cut across and artificial respiration be practised, it will be seen that the attacks of chorea remain stronger on the right than on the left side.

Trophic influence of the brain.—The experimental analysis to which the cerebral functions have been submitted has, in the first instance, displayed the relations of the brain with the muscular tissue, whose functional activity it

regulates ; later, these relations have been extended, like those of the nervous system itself, to a large number of other tissues (vascular and visceral muscles, visceral and cutaneous glands, etc.). This analysis is founded on the anatomical division of our tissues into special cellular orders very easy of recognition. But it is possible to proceed in a different manner. It is possible to take as a test of the brain's activity, not the different *tissues* which are to an unequal degree dependent upon it, but the *substances* excreted by the emunctories of the organism, which substances reveal the activity of the organism as a whole, and can therefore give us information with regard to the influence exerted by the brain on this activity.

This is the aim which Belmondo has in view. Brought back to the simplest terms, excretion presents itself under two forms having two distinct situations. The lung is the emunctory of *carbon* (carbonic acid) ; the kidney is the emunctory of *nitrogen* (urea and similar bodies). The experiment consists in measuring the gases of respiration, and also the total amount of nitrogen in the urine, first in the normal state and secondly after removal of the hemispheres. This experiment has been performed on pigeons, on which ablation with subsequent survival is easily performed.

a. *Excretion of carbon.*—The experiments of G. Corin and A. van Beneden had already shown that the removal of the cerebral hemispheres in pigeons does not sensibly modify the excretion of carbonic acid (nor the temperature) ; we have only to ascertain the facts with regard to the secretion of nitrogen. The experiment must necessarily be made on animals in a fasting condition, as during digestion, as is well known (in certain conditions), a notable quantity of nitrogen arising directly from the food is added to the quantity produced by the disassimilation of the tissues, and this must be eliminated.

b. **Excretion of nitrogen.**—Compared in fasting pigeons, some healthy and others deprived of the cerebrum, the excretion of nitrogen varies considerably, even to the point of being reduced in the second to less than half the value it has in the first. To put it otherwise, the brain governs in a certain manner and to a certain degree the excretion of nitrogen since, if it be removed, this excretion is diminished.

Nitrogen eliminated per kilogramme and per 24 hours.

Four first days of fast	Healthy pigeons	0·57
	Pigeons with cerebrum removed	0·27
	Ratio	0·47

The two principal excretions of the organism, carbonic acid by the lungs, nitrogen by the urine, have each a different signification. The first represents and measures the *waste of energy* of the organism : its principal source lies in the work of the muscles (although that of the other tissues helps slightly in the process) ; it is irregular, as are also the intermissions of this work itself. The second represents and measures the work of *disassimilation* of the tissues (including the muscular) ; it is constant as is this disassimilation itself.

In animals in a state of repose (in cages), the waste of energy is the same (very much reduced), whether they retain the brain or not. The difference is only marked when, the movements of both being unrestrained, the animals with brain intact can show their spontaneity. In the same animals in repose, some with, and others without the brain, we see, on the contrary, that disassimilation is much diminished in the last-named, and this is a new fact brought out prominently by these experiments. Thus the brain, which before had only been credited

with the possession of relations with the muscular tissue, is now seen to extend its action to the other tissues. Further, it not only regulates the waste of energy properly so-called (oxydation of the carbo-hydrates), but it also governs the molecular renewal of the elements (histolysis, dislocation of the albuminoids).

The regulative action of the waste of energy is, in certain determinate conditions, a conscious one. That of disassimilation is unconscious, and operates in the same way as ordinary reflex actions.

It must be admitted that any plausible explanation of the mechanism employed by the brain in the control of tissue disassimilation is absolutely lacking. In fact, though we are acquainted with nerves whose stimulation has for direct effect the augmentation of the waste of energy in the tissues and is displayed by an exaggeration of the excretion of carbonic acid (for example, motor nerves of the muscles), we know of none whose excitation would create an augmentation of their histolysis, to the extent of causing an exaggeration of the nitrogenous excretion. The relationship existing between the brain and what is called nutrition of the tissues (a relationship which facts seem to demonstrate, and which we have no reason to deny), cannot be interpreted in so clear a manner as can that existing between the brain and ordinary movement. Experimentally and logically, the intermediaries are unknown to us.

As a set-off, Goltz has observed in a dog from which he had removed the cerebral cortex great voracity and an exaggerated consumption of food. It is true that a notable part of this food must have been wasted, on account of incomplete digestion. However, the results of experiments differ from several points of view. This question demands fresh investigation.

BIBLIOGRAPHY.

Cerebellum.—Baginsky, *Arch. f. Phys.*, 1881.—Bechterew, *Arch. f. d. ges. Phys.*, 1884 et *Neurol. Centralbl.*, 1890.—Beevor, *Arch. f. An. und Phys.*, 1883, p. 363.—Borgherini et Gallerani, *Rivista sperim. di Frenatria et Med. leg.*, 1891.—Bouillaud, *C. R. Ac. sc.*, 1873 : *Arch. gén. de méd.*, 1827, t. XV, p. 64.—Chevreul, *C. R. Ac. sc.*, 1873.—Dalton—*Americ. Journ. of med. sc.*, 1861.—Dupuy, *Biol.*, 1885 et 1887.—Ewald, *Revue scient.*, 8 mai 1897.—D. Ferrier, La fonction du cerveau, et *Brain*, 1894.—Ferrier et Turner, *Proc. of Roy. soc.*, IV.—Flourens, Rech. expér. sur les prop. et les fonct. du syst. nerveux chez les animaux vertébrés, Paris, 1842.—Fodera, *Journ. de phys. expér.*, 1823.—Foville, Art. "Encéph.," *Dict. méd. et chir. pratiq.*—Laborde, *Biol.*, 1890.—Laborde et Duval, *Biol.*, 1875.—Leven et Ollivier, *Arch. gén. de méd.*, 1862–63.—Lapeyronie, *Mém. de l'Acad. des sc. de Paris*, 1741 ; *Journ. de Trévoux*, 1709.—Luciani, Il cerveletto. Nuovi studi di Fisiologia normale et pathologica, Firenze, 1891 ; *Arch. ital. de biol.*, 1894 et 1895.—Lui, Develop., *Arch. ital. de biol.*, 1894, t. XXI, p. 395.—Lussana, *Journ. de phys.*, V.—Luys, *Arch. gén. de méd.*, 1864.—Majendie, Précis élém. de phys., Paris, 1836, t. I.—Nothnagel, *Centralbl. Wissen.*, 1876.—Petrequin, *Gaz. méd.*, 1836.—Risien Russel, *Brit. med Journ.*, 1893 ; *Proc.*, 1893 : *Philos. Trans.*, 1894.—Pierret, Atrophie périph. avec lés. des olives, *Arch. de Phys.*, 1871–72, p. 765.—Rolando, Saggio sopra la vera struttura del cervello, Sassari, 1809 ; Osservat. sul cervellatto, Torino, 1828.—Serres, Anat. comp. du cerveau, t. II.—Schiff, *Recueil de mém.*, vol. III, 1896.—Stefani, Contrib. all. Fisiol. del Cerveletto, Ferrara, 1877.—Steiner in Vlassak, *Arch. f. Phys.*, 1887.—Thomas, Le cervelet . . . Paris, Steinheil, 1897 ; *Biol.*, 1896.—Vulpian, Leçons sur la physiol. gén. et comp. du syst. nerv., 1866.—Weir-Mitchell, *Am. Journ. of med. sc.*, 1869.

Movements of rotation—crura cerebelli, etc.—Belhomme, Mem. localis. fonct. fonét cérébr., Paris, 1838.—Gratiolet et Leven, *Arch. des sciences*, janvier-juin, 1868.—Longet, Traité de phys., 3e édition.—Majendie, Précis élém. de phys., Paris, 1836, t. I.—L. Petit, Les gangl. s. œsoph. escargot, *C. R. Ac. sc.*, 1888, t. CVI, p. 1809.—Pourfour du Petit, Revue d'obstétriq., d'anat. et de chirurg. de Louis, Paris, 1766.—Prévost, *Biol.*, vol. du cinquantenaire.

Optic thalamus.—Bechterew, Mouv. affectifs. *Soc. neurol et psych.*, Kazan, 1893.—Gayet, *Arch. de Phys.*, 1875.—Sellier et Verger, *Arch. de Phys.*, 1898, p. 706.

Corpus striatum.—Carus, *Journ. of comp. neurol.* 1895.—Francz et Pitres, *Biol.*, 1878.—Langley et Grünbaum, Ablat. écorce et corps strié dégénér., *Journ. of Phys.*, 1890.—Lehmann, *Arch. f. An. und Phys.*, 1886, p. 184.—Marinesco, *Biol.*, 1895.—Hale White, *Journ. of Phys.*, 1890, p. 1.

Internal capsule and centrum ovale.—Carville et Duret, *Arch. de Phys.*, 1875, p. 136.—Etienne, Monoplégie faciale et dév. conjug. des yeux, *Presse méd.*, 1896.—Pitres, *Arch. clin. de Bordeaux*, 1893.—Veyssière, *Arch. de Phys.*, 1874, p. 288.

Corpus callosum.—Lo Monaco, Calleux et gangl. basilaires, *Arch. ital. de biol.*, 1897, t. XXVII, p. 296.

Comparative anatomy.—Ad. Bary., Dévelop. des centres, *Arch. f. An. und Phys.*, 1898.—Chatin, Homologies, poissons, *C. R. Ac. sc.*, 1889, t. CVIII, p. 628.—Dhéré et Lapicque, *Arch. de Phys.*, 1898, p. 763.—Faivre, Insectes centres nerv. mouv. rotatoire, *C. R. Ac. sc.*, 1875, t. LXXX, p. 739, 1149 et 1332.—Fritsch, Homologies, *Arch. f. An. und Phys.*, 1877.—Giacomini, Microcéphales, *Arch. ital. de biol.*, 1891, t. XV, p. 63.—Lussana, Neurophys. comp., *Arch. ital. de biol.*, 1883, t. IV, p. 283.—Schlapp, Différ. de struct. *Arch. f. An. und Phys.*, 1898, p. 381.

Excitability of the cortex—different influences.—Aducco, *Arch. ital. de biol.*, 1889, t. XI, p. 192, 1891, p. 136, et 1893, p. 1.—Axenfeld, Subst. chim., *Arch. ital. de biol.*, 1895, t. XXII, p. 60.—Bechterew, Inflammation, *Messager neurol.*, Kazan, 1894.—Bochefontaine, Déplacement des points excitables, *Arch. de Phys.*, 1883, p. 28.—Br.-Séquard, Vivisect. sur homme, *Arch. de Phys.*, 1875 et 1890, p. 762.—Carvalho, Cocaïne, *Biol.*, 1888, p. 664.—Charpentier, Cocaïne, *Biol.*, 1884, p. 758.—Couty, *Biol.*, 1880, p. 44 ; 1886, p. 164.—Danillo, Alcool ; absinthe, *Biol.*, 1882, p. 83.—Franck et Pitres, *Arch. de Phys.*, 1885 ; *Biol.*, 1878 et suiv.—Heimann, Wirkung d. Drucks . . . *Arch. f. An. und Phys.*, 1884.—Joukoff, Arrêt de la circul. céréb., *Bolnitch. Gaz. Bot.*, 1895 ; *Cliniq. malad. ment.*, Saint-Pétersbourg, 1895.—Langlois, Centres psycho-mot. nouveaunés, *Biol.*, 1889 p. 503.—Munck, Anémie, *Arch. f. An. und Phys.*, 1883.—Openchowski, Act. du froid, *Biol.*, 1883.—Orchansky, Anémie, *Arch. f. An. und Phys.*, 1883.—Teschich, *Arch. de Phys.*, 1885.—Thomasini, Section des racines postérieures, *Arch. ital. de biol.*, 1895.—F. Franck et Pitres, Div. communications, *Biol.*, 1878.—De Varigny, *C. R. Ac. sc.*, 1884.—Vulpian, Durée après la mort, *C. R. Ac. sc.*, 1885.

Mechanical stimulation of the brain.—Couty, *Biol.*, 1880, p. 46 ; excitation thermique, *Biol.*, 1886.—Luciani, *Arch. ital. de biol.*, 1883, IV, p. 268.—Vulpian, *C. R. Ac. sc.*, diverse notes, 1885.

Anatimico-clinical methods of observation.—Charcot et Pitres, *Arch. neurol.*, XXVII, 86, 1894.

Inhibitory power of the cortex.—Fano, *Arch. ital. de biol.*, 1895, t. XXIV, p. 438.—Libertini, *Arch. ital. de biol.*, 1895, t. XXIV, p. 438.

Latent period.—Fr.-Franck, Localisat. cérébr.—Novi et Grandis, *Arch. ital. de biol.*, 1888, t. X, p. 314.—De Varigny, *Arch. de Phys.*, 1885.

Refractory period.—Broca et Richet, *Biol.*, 1896.

Cerebral localizations.—Discussion.—Albert, *Wien. med. Presse*, 1895.—V. Borosnyai, Luchsinger, Steger, Pestalozzi, Hermann, *Arch. v. Pflüger*, 1875, t. X, p. 77 ; Byron Bramwell, *Sem. méd.*, 1896.—Charcot, *Biol.*, 1875, 1876.—Couty, *Arch. de Phys.*, 1883 ; *C. R. Ac. sc.*, 1879 et 1881.—Charcot et Pitres, *Arch. clin. de Bordeaux*, septembre, 1894.—Debierre, *Biol.*, 1888.—Dupuy, *Biol.*, 1875, 1886, 1887, 1888.—Duval, Rapport d'une commission, *Biol.*, 1886, p. 371.—Eisenlohr, *Deutsch. Zeitsch. f. nerv. Heilkunde*, 1893.—S. Exner, *Journ. of Phys.*, 1880.—Golgi, *Arch. ital. de biol.*, 1888.—Huglings Jackson, Fragments neurologiques, *Lancet*, 1893.—Jackson (de Boston), Perforation du crâne de part en part, pas d'aphasie, survie 10 ans, attaque d'épilepsie, *Biol.*, 1871, p. 169.—Marcacci, *Biol.*, 1882 ; *Arch. ital. de biol.*, 1882, t. I et II.—Marinesco, Revue, *Sem. méd.*, avril, 1896.—Munck, Critiq. des vues de Goltz, *Soc. de phys. de Berlin*, avril, 1896.—Pick, *Prazer Zeitsch. f. Heilk.* X, 1, 138.—Pitres, *Biol.*, 1876 ; *Congrès de Nancy*, 1896.—Schiff, Lez. de Fisiol. sist. nerv. encefalico, Firenze, 1873.

Localization of speech.—Bouillaud, *C. R. Ac. sc.*, 1873.—Broca.—Chevreul, *C. R. Ac. sc.*, 1873.—Fournie, *C. R. Ac. sc.*, 1873.

Cerebral localizations—Motor centres.—Bechterew, Excit. chez l'homme, *Arch. f. An. und Phys.*, 1889, sup. p. 943.—Carville et Duret, *Arch. Phys.*, 1875.—Couty, *Arch. Phys.*, 1879, 1881.—Couty et Lacerda . . . Curare . . ., *C. R. Ac. sc.*, 1880, t. XCI.—Ed. Hitzig, *Reich. und Du Bois R. Arch.*, 1870, Heft 3 et 4 ; Unters. ub. d. Gehirns (Abhandl. physiol. und path. Inhalts), Berlin, 1874.—G. Fritsch und Ed. Hitzig, Ueb. elektrish. Erregb. der Grosshirns, *Reich. und Du Bois R. Arch.*, 1870, Heft 3.—Ferrier, *Brit. med. Journ.*, avril, 1873 ; *Progrès méd.*, 1873.—H. Jackson, *Med. Tim. and Gaz.*, 1861 et suiv.—Lépine, Thèse agrégation, 1875.—Lussana et Lemoigne, *Arch. Phys.*, 1877, p. 119.

Localization of general sensibility and of temperature.—Bechterew, *Arch. f. An. und Phys.*, 1900, p. 22.—Brissaud, Leçons Salpêtrière.—Br.-Séquard, Anesthésie, *Biol.*, 1883.—Darkschevitsch, *Neurol. Centralbl.*, 1890.—Dana, *Journ. of nerv. and ment. dis.*, 1894 ; *Medic. Record*, N. York, 1893.—Dejerine, *Revue neurol.*, mars, 1893 ; Étude sur l'aphasie, *Revue de méd.*, 1885 ; *Arch. Phys.*, II, 588.—Dessoir, *Arch. f. An.*

und Phys., 1893, p. 525.—Dupuy, *Biol.*, 1886.—Ferrier et Yeo, 1875 à 1884.—Franck Hochwart, *Soc. med. de Vienne*, 1893; *Internat. klinish. Rundschau*, No. 9, 1893.—Franck, S. Madden, *Journ. of nerv. and ment. dis.*, 1893.—Marinesco, Revue, *Sem. med.*, 1896.—W. Mott, *Journ. of Phys.*, 1894.—H. Munck, Ueb. die Funct. der Grosshirn., 1890; Ueb. die Fühlensphär., 1892.—Ransom, *Brain*, 1892.—J. Soury, *Rev. gén. des sc.*—Schaffer, *Journ. of Phys.*, 1898.—R. Tripier, *Congrès de Genève*; *Revue de méd.*, 1880.—Vulpian, Sensibilité des lobes du cerveau, *C. R. Ac. sc.*, 1882.

Removal of the cortex—Degeneration.—Langley et Sherrington, *Journ. of Phys.*, 1884. vol. V, p. 49.—Sherrington, *Journ. of Phys.*, 1889 et 1890.—Pitres, *C. R. Ac. sc.*, 1884.—Sanarelli, Processus de réparation, *Arch. ital. de biol.*, t. XIII, p. 490.

Reappearance of movements after destruction of the cortex.—Arloing, *Biol.*, 1880.—Goltz, Mémoires divers.—Ferrier, Les fonctions du cerveau.—Vitzou, *Arch. de Phys.*, 1897.

Reappearance of paralyses under the influence of different causes (Anémie, anesthésiques).—R. Tripier.

Post-anæsthesic paralyses.—Verhogen, *Journ. méd. de Bruxelles*, 1896.—Vautrin, *Congrès de Nancy*, 1876.

Various localizations in man.—Charcot et Pitres, Centre du relèvem. de la paupière, *Arch. de Bordeaux*, 1894.—De Bosco, Relèv. paup., *Revue de neurol.*, 1893; Il Pisani, *Gaz. Sicula*, fasc. I, 1893.—Brissaud, Hémiplégie faciale particip. de l'orbicul., *Progrès méd.*, 1893.—Féré, Tic douloureux de la face, lésion du pli courbe, *Biol.*, 1876.—Gauché, Monoplégie brachiale, hémipl. fac., *Biol.*, 1879.—Hester, Ramoll. pli courbe, ptosis gauche, *Journ. of nerv. and ment. dis.*, 1895.—Joffroy, Monopl. membr. inf. ram. lob. paracent., *Arch. Phys.*, 1887.—R. Tripier, Lésion rolandique gauche, hémiplégie droite, conservation mouv. de la face, *Soc. sc. méd. Lyon.* 1865.

Various localizations in animals.—Beevor et Horsley, *Arch. de neurol.*, *Biol.*, 1887.—Rethi, Mastic. déglutition, *Wien. med. Presse*, 1894.—Richet, Réflexe de direction de l'oreille, *Biol.*, 1886.—Sherrigton, Centre du pouce; centre de l'anus, *Congrès de Liége*, 1892.—Vitzou, Centre visuel du chien, *C. R. Ac. sc.*, 1888, t. CVII, p. 279.—Werner, Mouv. tronc et nuq. chien, *Allg. Zeitsch. f. Psych.*, 1895.

Centres of phonation; of the larynx.—Brœckaert, 6e *Congrès otolaryngolog. belge*, 1895.—Charcot et Pitres, *Arch. clin. de Bordeaux*, 1894.—Krause, *Arch. f. An. und Phys.*, 1884; *Brit. med. Journ.*, 1889.—G. Marini, *Real. Acad. med. chir. d. Genova*, 1893, analysé par Garel, *Province méd.*, 1894.—Onodi, *Berlin. klin. Wochensch.* 1894.—Semon et Horsley, *Brit. med. Journ.*, 1889, I.

Pseudo-bulbar paralysis.—Hallipré, *Thèse Paris*, 1894.

The brain and nutrition—Temperature of the brain.—Mirto, *Arch. ital. de biol.*, 1899, t. XXXII, p. 335.—Mosso, *Crownian Lectures*; *Arch. ital. de biol.*, 1893, t. XVIII, p. 277, et 1895, t. XXII, p. 264.

Cerebral circulation.—Bayliss, L. Hill et Lowell Gullard, Press. intr. cran. circul., *Journ. of Phys.*, 1895, vol. XVIII, p. 334.—Cavazzani, Circul. collat., *Arch. ital. de biol.*, 1891, t. XVI; Action de l'asphyxie, *Ibid.*, 1893, t. XVIII, p. 54.—Duret, Étude anatom., *Arch. Phys.*, 1874.—L. Hill et Macleod . . . Supposed vasomot. . ., *Journ. of Phys.*, 1901, p. 394.—Roy et Sherrington, Régulat. circul. cérébr., *Journ. of Phys.*, 1890, p. 85.—Rummo et Ferrannini, Circ. cér. chez l'homme, *Arch. ital. de biol.*, 1889, t. XI, p. 272.

Influence of the brain on the circulation.—Binet et Vaschide, Pression du sang chez l'homme, *C. R. Ac. sc.*, 1897, t. CXXIV, p. 44.—Mosso, Mémoires divers.—Thanoffer, *Arch. v. Pflüger*, 1879, t. XIX, p. 254.

Influence on heat.—Voy. *Chaleur animale.*

Influence on organic life.—Bechterew, Pupille, *Arch. f. An. und Phys.*, 1900.—Bechterew et Mislawsky, *Arch. f. An. und Phys.*, 1889, sup., 1891, p. 380.—P. Bert, Coloration de l'axolotl, *Biol.*, 1879, p. 65.—Bochefontaine, *Arch. Phys.*, 1876. Couty, *Arch. Phys.*, 1876.—Judée, Salivat., *C. R. Ac. sc.*, 1887, t. CV, p. 893.—Herl. Parsons, Dil. pupille, *Journ. of Phys.*, 1901.

Disturbances in the exchanges.—Belmondo, Échange azoté, *Arch. ital. de biol.*, XXV, 3, 481.—D. Franck, *Arch. f. An. und Phys.*, 1900, p. 209.—L. Hill et Nabarro, Éch. des gaz, *Journ. of Phys.*, 1895, vol. XVIII, p. 218.—Stcherbach, Éch. ac. phosphoriq., *Arch. méd. exp.*, 1893, No. 3.

Trophic disturbances.—Joffroy . . . à la suite lésion lobe occipital, *Biol.*, 1875, p. 399.—Langlois et Richet, Troubles trophiq. bilatéraux après lésion de l'écorce cérébrale, *Biol.*, 1890, p. 315.

SECOND SECTION

Special Innervations

If we take as a foundation either the different sensations which are aroused in us by external provocations, these also differing in their nature and mode of action, or the motor phenomena which are most directly associated with these sensations, we may divide innervation into five great systematizations, or principal categories, which will be *visual* innervation ; *auditory* innervation ; *tactile* innervation ; *olfactory* innervation ; *gustatory* innervation.

Sensation is, in fact, the quality which is most characteristic of the nervous system ; this latter being, of all the tissues, that which displays it in the highest degree, and which, on account of its complexity and its organization, confers on it its highest value. This first conception is a matter of ordinary knowledge. On the other hand, all sensation is intimately connected with motor actions, which may effect areas of the nervous systems at the same time various and distant, but of which some are immediately dependent on these sensations, and, as such, are characteristic of them. *Each sensory system is a sensitivo-motor apparatus,* which, in a certain measure, is not isolated from the others, but capable of being so isolated ; that is to say, is complete in itself. *Functional links exist between these partial systems,* so as to ensure the unity of the nervous system, and by it the unity of the living being. This second conception, which sanctions the intimate connexion between sensation and motion, has begun to be generally adopted. Finally, sensation allows of an infinity of degrees and of gradations from those which have their fullest expansion in the superior senses, down to those quite obscure ones which interpret our most elementary requirements. In writing a complete history of the nervous system it becomes necessary to connect these subconscious (sometimes called unconscious) sensations with the motor acts related to them, to the distinct sensations of the superior senses, according to their functional affinities. This idea of an obscure consciousness governing all living actions, even those which appear quite mechanical and automatic, is the most modern of all those we have passed in review, and daily gains more adherents.

Specific activities.—The nervous system is an assemblage of partial systems, each, in an isolated manner, presiding over some function of a determinate nature. None of these can replace any of the others, or be replaced by them. This partition stands out very clearly when the nervous system is considered at its periphery, either at the point of arrival or of departure of the stimuli by which it is traversed : it becomes more and more obscure in proportion as we penetrate the depths of the system ; of this statement the question of cerebral localizations is a proof. We shall then start from the extremities of the nerves, ascending nearer and nearer to the brain, tracing in this way, according to their kind, the great divisions and subdivisions of the nervous functions. The sensory field is particularly favourable for the determination of this kind of division.

1. **Sensory field ; its divisions.**—The sensory field is divisible at the periphery into five parts, corresponding to the five senses. Each sense is adapted to a particular sort of stimulation, we may even say to an exciting medium of a special nature, to a *specific* excitant which cannot be replaced by that of another sense. Out of the infinitely varied movements by which it is surrounded, our organization has chosen five particular orders : these are the source of all our knowledge.

The *retina*, or sensitive membrane of the eye, obeys the vibrations of the ether, that body which penetrates all others, and is distinguished from them by its imponderable nature.

The *internal ear* is sensitive to the vibration of sonorous bodies, and, above all, of the air, another elastic medium, eminently suitable for the propagation of an undulatory movement to a distance.

It must be observed that, among the undulatory movements of the air, as of the ether, our organization is not restricted to, or has not succeeded in adapting itself, to all, but only to a small number amongst them, to those for the ear, which are comprised between 32 and 50,000 vibrations in the second, about eleven octaves ; to those for the eye which are comprised between 450 to 880 trillions of vibrations the second. But as these media are traversed in all directions by vibrations of every length which co-exist and are superposed without being confounded, this restriction does not imply any difficulty or real gap in the exercise of the senses.

The organs of *taste* and *smell* are affected by excitants whose physical nature, modality and medium of propagation are absolutely unknown to us, but which it is possible to conceive of as being also vibratory changes of a special nature.

The *skin*, which is the organ of *touch*, is affected by the contact of more or less resisting bodies, and also by those undulatory movements to which we give the name of *heat*. In this sense, which is less specialized than the others, all ordinary excitations are included, such as tensions, compressions and modifications of whatever nature which affect our superficial or deep organs and belong to the *sensibility* called *general*.

2. **Specificity of the stimulus.**—Each of these excitants is *specific*.

Excitation is a shock, a communicated movement; we learn from physics that a vibratory movement is not communicated from one body to the other, unless *resonance* exists, that is to say, an agreement between the vibrations of these two bodies. The organs of the senses are essentially *resonators*, the word being taken in its most general sense. The retina and the ear are alike irresponsive to any shocks except those which, both as regards quality and amplitude, are appropriate to them.

Adaptation of the senses to their specific excitants; appropriated resonators.—Being a portion of the ectoderm which is developed with a view to the performance of special functions, each organ of the senses is provided with a special resonator. The shock of the external medium, when it transgresses certain limits, is non-existent for the resonator; but when it possesses the right tonality, it finds a gate of entrance in this sense and penetrates the nervous system, where it finds itself in conflict with a crowd of others, and, remaining there a longer or shorter period, leaves it in the condition of a motor phenomenon.

But, before leaving, it gives rise in the depths of the nervous system, to a fact which we call psychical, or one of sensibility, in one word, to *sensation*, in opposition to the physical fact of *impression*.

3. **Specific nature of the sensation.**—We have said that *impressions are specific*, and we may add that *sensations are also specific*, for to each particular modality of impression a particular modality of sensation corresponds. Before ending in the deepest part of our being, in the most abstract notion of general ideas, which has the conflict of sensations for its origin, these latter put to port somewhere in the nervous system; there is therefore a functional partition of sensations, as there is one of impressions.

Sensation, a fact of purely internal observation, can only be defined by its contrast with the psychical fact of impression. It is not in the very least a geometrical representation of the physical changes which give birth to it. The ignorant person who can distinguish between a sound and a colour has not the least conception of a sonorous or luminous vibration; the educated man alone is acquainted with this detail, or believes that he can explain it.

Sensation results from an association of stimuli. It is a synthesis of these stimuli effected in the nervous system.

Uniformity of function of the nervous elements.—Further, we may add that a shock of a particular sort which has arisen in a sensitive or sensory resonator is never transmitted to the brain by the sensitive or sensory nerves, retaining its original character. All these shocks, specific in their origin, are brought back to a single, or at any rate to

almost an uniform state, the *nerve wave*, as soon as they enter the nervous system properly so called. The nerve wave (with some trifling differences) appears to be of the same general form, or, in a word, of the same nature, in all nerves (sensory, sensorial or motor). *Each neuron, taken by itself, is functionally equivalent to any other neuron ;* there are not any specific neurons, properly so called.

Specificity of the neurons.—The data furnished by morphology and experiment have so far pointed to the predominance of fundamental resemblances between nerve elements, rather than to real differences between them, except as regards those which are contingent and without known relation with the function of these elements. There must, however, exist between one and the other, certain quantitative or qualitative modifications, in order that these elements, by being associated, should be able to form functionally differentiated systems. These modifications may bear only on characters which are but little obvious and be themselves individually very unimportant. The multiplicity and the complexity of the associations are sufficient to enlarge them and to elicit from them very dissimilar effects. On the other hand, these modifications may be confined to certain parts of the neurons, for example, to their extremities in the areas by means of which they become associated the one with the other. In fact, more notable and more significant differences are discoverable in their polar fields than in their axons or their cell bodies.

Further, we are ill equipped for the struggle required in order to seek for and understand these differences. The nerve wave, of which so much is heard, is almost unknown to us as regards its real form. Some facts about its rate of progress are all that we possess.

Experimentally, our ideas on this point are based on the two following facts : (1) *The nerve fibre, which is a continuation of a sensory apparatus, is generally refractory to the specific excitant of this sense.* From this it follows that the sensorial apparatus is both a resonator adapted to the external excitant, and a transformer of the excitation which adapts it, in its turn, to the nerve which follows it. (2) *All the nerve fibres, to whatever sense* (function) *they may belong, are capable of receiving certain excitations different from the specific ones*, and which, for this reason, are called *ordinary*, or *general stimulations* (pinching, chemical action, electricity, etc.). Whence it follows that these fibres, having received this ordinary excitation, develop a specific sensation in the system to which they belong.

It is obvious that the optic nerve is not a channel for light, nor the acoustic nerve for sound. But the component elements of each of these two nerves have not, as regards structure or properties, anything which distinguishes the one from the other, or from all the other nerve elements. They possess the common excitability of the latter, but nothing else. The luminous ray appropriate for the stimulation of the retina has no effect if immediately thrown on the optic nerve ; the sonorous wave is without effect on the acoustic nerve ; and this because the adaptive apparatus is lacking in both cases. But, on the other hand, ordinary, commonplace excitations of the nervous system, such as pressure, pinching, electrization, excite these just as all other nerves, and so give rise to specific sensations corresponding to the specific excitant of the senses to which they belong.

Examples.—Pressure on the trunk of the optic nerve gives rise to a luminous sensation. In the operation of enucleation of the eyeball the patient perceives flashes of light, resembling lightning (Tortual) ; only, however, on the condition that the fibres of the optic nerve have not undergone atrophy. A slight pressure

on the ball of the eye towards the edge of the retina causes the appearance of a subjective image of the body compressing it ; this is what is known as a *phosphene.* By turning the eye firmly downwards under the closed eyelids and lightly sliding the tip of the first finger under the orbital arch, across the upper eyelid, a phosphene is created which is perceptible at the lower part.

Shocks brought to bear on the temporal bone may, at the same time, excite the acoustic nerve in a mechanical manner, and create a sonorous sensation.

Electrical stimulation applied to the different sensory nerves may also give rise to the sensation proper to each of the senses to which they belong. In a word, excitants which have nothing specific about them, general excitants, that is to say, those capable of affecting all the nerves, create specific sensations when they can find the entrance to special systems corresponding to the different senses.

Definite relation between impression and sensation.—*Sensation with its specific characters may then exist in us in the absence of the particular excitant with which it was originally connected.* This is proved, not only by the preceding analysis, where an ordinary excitant is seen to penetrate artificially into one of our sensorial systems, but also in a very simple manner by the fact that sensation is preserved in us in a state of residue or of remembrance after the external excitant has disappeared. Indeed, this fact of conservation implies that sensation has means appropriate to the nervous system of being created quite independently of the presence of the habitual excitant. According to the statement of J. Müller, what we feel is, *the state of our nerves.* We can feel nothing outside of us except by this state of our nerves, and we can continue to feel this state after the cause by which it has been elicited has either ceased, lost its specific value, or been replaced by an ordinary cause.

There are within us sensorial systems which react specifically to every stimulus which reaches them. These systems, at their surface of contact with the exterior, are furnished with special apparatus (organs of the senses) which select, from the excitatory shocks of every form and origin by which we are surrounded, those which can in an isolated manner penetrate into each of these systems to the exclusion of the others. Thus is created for us a determinate relation between each order of sensation and the external excitant from which it originally arose. This relation is an empirical one, but is sufficient for the daily requirements of existence ; it teaches us all that is necessary for us to know, but not concerning everything external to ourselves. By the comparison of the information furnished by the different senses, these indications being subjected to verification and criticism, we are in a position to make a distinction between our actual and our reawakened sensations or remembrances ; we also make the same distinction between the normal and regular external sensation and that which is artificial and irregular. When this criticism is wanting, there is *hallucination.*

Sensation is a phenomenon of evolution ; it is at the same time both a process and a progress ; it takes place in a system composed of successive and at the same time parallel elements, which are associated according to relations special to it and of a very complicated order. In the same way as the system which acts as its support, it is formed of numerous elements which are none other than the particular activities and the states of excitation of the parts composing this system, co-ordinated according to a law which is special to it. We have said that the stimulus invades the system and advances therein in the fashion of a wave, whose form becomes more and more complicated in proportion as it approaches and reaches the cerebral cortex. In this forward march of the impulse, where is the precise locality of sensation ? Has it an exclusive and defined habitation ? What parts are sufficient for or necessary to it ? What does experiment tell us on this subject ? How are the facts which it has displayed to us to be interpreted ?

An effort has always been made to arrange the recognized facts concerning the structure of the nervous system in accordance with the information furnished by observation.

Interpretations have necessarily varied according to the state of our knowledge on these points, and also with the general theories obtaining in biology.

Former scheme.—The three data essential to observation are : (*a*) the specific nature of the impression, implying a specificity of the receptive organ of the senses : (*b*) uniformity of function of the nerve fibres, contrasting with the specificity of the receptive element : (*c*) specific nature of the internal phenomenon of sensation, contrasting in its turn with the uniformity of the transmitting elements. With regard to these data, the following anatomical scheme was quite recently accepted as summing up the structure of the nervous system, namely : (*a*) a peripheral cell adapted specifically to the excitant of each given sense ; (*b*) a fibre, possessing the activity common to all fibres, transmitting the impression received from its origin to its termination ; (*c*) a central cell with a specific function, realizing the internal phenomenon of the sensation.

As will be obvious, this scheme distinguished the existence of two kinds of elements in the nervous system : the fibres and the cells. Uniformity was allotted to the first of them, and specificity to the second. This specificity was, in its turn, again divided into two kinds : physical specificity, appertaining to the peripheral cell (adaptations to a shock of a determinate nature), psychical specificity to the central cell (sensation of a determinate nature).

Thus sensation was considered to be a cellular function, like impression itself, and transmission a function of the fibre, which was thought to be an element distinct from the cell.

Its insufficiency.—This theory crumbled away with the anatomical thesis which served it as a support. We no longer admit the existence of two nerve elements (the cell and the fibre), but only of one (the neuron, which is a cell provided with fibrillary poles). The division between nerve elements is not, as was formerly supposed, between the cell and the fibre, but between the terminal and initial ramifications of the neurons. The pathway of the nerve wave giving rise to the sensation is not a simple fibre stretched between two cells, one peripheral

and the other central; but is formed by a series of neurons placed end to end. The junction of these neurons is not made unit by unit, pole by pole, but by a complicated arrangement, the terminal polar field of each antecedent neuron according with the initial polar fields of a great number of consecutive neurons; and reciprocally. The dividing surface which outlines the locality of these junctions is not simple, but enormously twisted and complicated; because, in addition to the direct contacts between neurons of great length, there are other indirect ones effected between neurons of short or medium length; thus these associations are multiplied to an infinite degree. Finally, this complication of the paths followed by the impulse, is not uniform, but increases as it approaches the cortex, and is renewed on leaving the latter in order to gain the motor organs.

Of the former theory this much, however, is true, namely, that the physical specificity of the impression is united to a determinate cellular function (organs of the senses): on the other hand, under a slightly altered form, we retain the conception of uniformity in the function of neurites (or fibres of neurons). But that which appears to be destroyed for ever is the conception of sensation as being a cellular function. *Sensation is a systematic function.* The more clear, conscious and refined it is, so much the more complicated and highly developed is the system which serves as its support and lends itself to its evolution. The proof of this will be established by comparing the systems in which reflex sensibility is observed to develop, both that called instinctive and that which is strictly conscious, which systems define the three principal limits of the gradation of psychical phenomena.

Unity of the sensation; its determinative condition.—Sensation is a phenomenon which impresses us by its unity; the nervous system and the component systems which it includes are, on the contrary, distinguished by their complexity. Hence, no doubt, arises the repugnance which has been felt to attaching and superposing the first of these to the second; and, by a logical consequence, the converse tendency to imprison sensation in the smallest known biological element, namely, the cell (the nerve cell). But since analysis has penetrated this so-called element, it has become necessary to recognize how far removed it is from simplicity. Unity of sensation explained by unity of the cell is a pure delusion.

For ourselves, our nervous system is one and indivisible; this is because we comprehend it with our *internal senses*, which precisely realize its analyses or its syntheses. On the contrary, the nervous system of one of our fellow-creatures appears to us in all its complexity; this is because we grasp it with our *external sense* which is capable of analysing it. In the first case the nervous system is ourselves, that is to say, the subject, on which its quality of sentient being confers its unity. In the second case, the nervous system is outside ourselves, that is to say, an object which we can divide into as many partial beings as the power of our means of analysis permits. The two operations employ different and in no way superposable modes of procedure. The internal sense, like the external senses, proceeds by analysis and by synthesis; but their situation in relation to each other is such that the one often builds up that which the other analyses, and reciprocally. An absolute harmony between the two would cause all the practical benefit which we draw from the arrangement to be lost.

Seat of sensation.—If, again, we represent to ourselves the impulse

advancing in the nervous system after leaving an organ of the senses, we ask ourselves at what point of its journey, at what precise halting place in its path, does it become a sensation ? The answer usually is : in the cerebral cortex. The brain's cortex is not an ideal surface, but comprehends, in itself alone, complicated systems which are attached to other antecedent and consecutive systems. Experiment points out the cerebral cortex as being a locality of nervous matter possessing essential functions as regards the development of sensation. From this point of view the analyses which are carried out by mutilations of the two extremities, or, still better, of the roots (organs of the senses) and the summit of the nervous system (cerebral cortex) are very instructive.

If we assume that an organ of our senses is suppressed, impression and stimulation cannot in the future be renewed (except in a very incomplete and artificial manner) ; but observation teaches us that they still persist in us, though more or less weakened and in an indefinite manner (the blind person sees in himself forms and colours, remembrances of his former impressions, etc.).

If we imagine the cortical area corresponding to one of our senses obliterated, impressions would continue to flow in upon us with the same abundance and the same intensity as before, but clear sensation, conscious and personal sensation, would be lacking. Has this fact caused the total disappearance of all possibility of sensation ? This was for a long time held to be the case, and this belief was founded on the extraordinary diminution of psychical phenomena resulting from extremely superficial mutilations of the brain. But it must be recognized that the destruction of the cortex allows an instinctive consciousness to subsist which is presided over by the inferior regions of the brain, just as the destruction of these regions, in its turn, allows of the subsistence of a reflex activity which in itself is a weakened instinct, or the rough sketch of an instinct. The law of continuity, which has nowhere so many applications as in the living being, is here clearly displayed. The development of sensation has roots deep down in the inmost structures of the nervous system. Of whatever nature it may be, and in whatever degree we consider it, sensation does not arise all at once, in an abrupt manner, amongst the particular elements belonging to an exclusive area of this system ; but it is being prepared during the whole length of the paths which it traverses, is progressively developed in its course, and is finally completed on arriving at its summit. Each element invaded by the impulse adds its contingent of activity in a determinate order to this organization, which progressively increases, and which, when realized, is sensation.

Sensation considered with regard to time.—Considered with regard to space, sensation was formerly supposed to occupy only an exclusive and restricted position in the nervous paths which are traversed by the impulse. We now give it a wider extension by assigning to it a preparation, a development and a completion. Considered with regard to time, it has equally, from the very fact of the progression of the impulse through the nerve paths, a limited duration ; but from this point of view a distinction must be made between the strong or

actual sensation, and the remembrance or *re-awakened* sensation, whose intensity is feebler.

Data yielded by experiment show that the strong sensation exceeds in duration the impression which has given it birth (example : the persistence of retinal impressions, or, to put it better, of optic sensation). This fact is in harmony with the theory of the development of sensation : the synthesis of its component elements being accomplished during the progression of the impulse, just as happens with regard to its time of extension in the system.

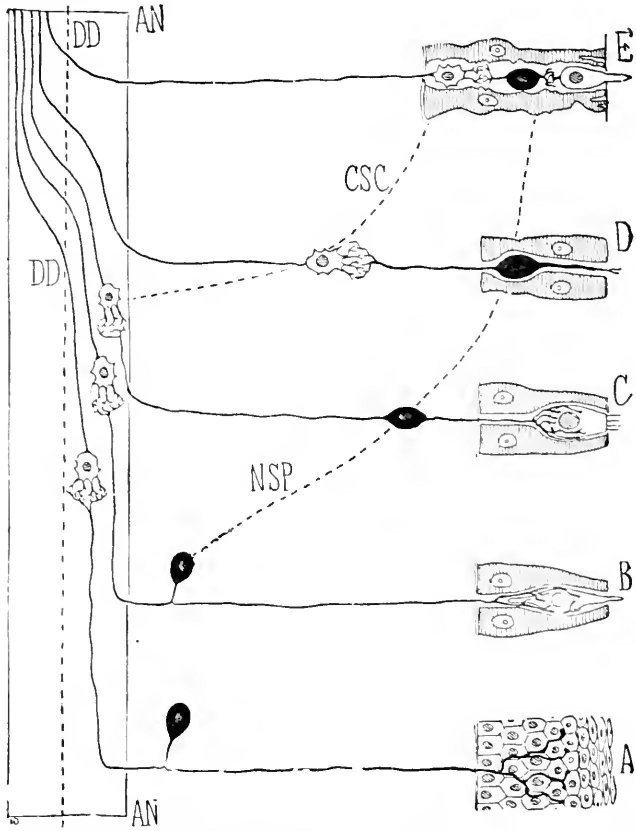


FIG. 206.—General arrangement of the centripetal paths of the different senses and their morphological differences.

Two neurons placed in succession ; peripheral neuron (cell in black) ; deep neuron (cell in white).

A, general sensibility ; B, taste ; C, audition ; D, olfaction ; E, vision.

The dotted line NSP indicates the displacement of the peripheral neurons towards the periphery starting from that of audition (C).

The dotted line CSG marks the same change of position for the deep neurons starting from that of olfaction (D).

AN, nerve axis ; DD, decussation of the axis cylinders of the deep neurons.

Specific nature of the sensorial systems. — The sensation corresponding to each sense (visual, auditory, tactile, sensations, etc.) is developed in a particular system retaining, up to a certain point, its dependence and its distinct limits. Each of these sensations has its special qualities, this being the reason why it is called specific : the system which gives it support must then also be specific. Like the sensations themselves, these systems display in their constitution features common to

all, and should at the same time present particular ones from which each derives its specific nature. Only, in a manner contrary to that existing for sensations, in which the specific characters are the most obvious, it is in these systems the points of resemblance which are easiest of recognition; this results once more from the difficulties of an opposite nature which are encountered by analysis, whether it be of sensation itself or of the anatomical system in which its evolution is carried out.

The visual, auditory, tactile, olfactory and gustatory systems are constructed of the same elements, the neurons, on the same general morphological plan recognizable in each of them. They present, it is true, markedly obvious differences of form, but these external and contingent differences do not explain the differences of their function.

The functional specificity of each of them depends in all probability on the particular modality of the relations contracted by their component elements, as well as by the primitive systems associated by them.

Motor specificity.—At the terminal extremity of the nervous system, whence stimuli proceed to produce their ultimate effect, we find peripheral organs formed of cells adapted to a corresponding motor function. These organs are subdivided into two large groups, each of which discharges an important function; (1) Muscles whose function is above all energetic, and (2) Glands whose function is more particularly chemical, that is to say, elaborative of particular products. The first are the organs of a movement which is especially massive and amplified; the second those of movement more particularly molecular, although in both these two orders of movement are represented.

The essential function of the one is, in fact, *contraction*, that of the other, *secretion*. Both one and the other of these two functions, especially the second, present diverse and varied modalities, and owing to this fact they are specific.

By the help of the muscles and of the glands, the excitatory cycle, after having passed through the phases above described, terminates in acts of a pre-eminently physical nature. Born in the physical world, it returns thither and is there consummated. These final actions, taken individually, represent cellular functions. But, considered in their relationship with others, they represent more or less complicated co-ordinated acts; in a word, systematic acts; this co-ordination, or systematization still being the work of the nervous system, which distributes the impulse to these motor apparatus in a determinate order.

CHAPTER I

TACTILE INNERVATION

Cyclic system.—The system which serves as a basis for tactile innervation, like all analogous sensory systems, and like the nervous system in its entirety, is necessarily a cyclic one, which receives movement, transforms it, retains it as long as it chooses, and then restores

it to the medium from which it first received it. This system is not invariable in its limits and its direction, but its connexions with other similar systems permit of its borrowing their paths of return, so as to increase still further the variety of the motor reactions. However, it is possible to recognize paths of reflexion which are in some sort natural and habitual to it, and which, after making the reservations mentioned above, will serve to round off its description.

Its extension to the deep organs.—In spite of these restrictions, it is necessary to understand that the system thus defined is graduated as concerns its constituents, like the sensibility to which it acts as a support. Nothing is clearer than the connexion between movement and sensation in the action of feeling a body with the hand. In other areas of the skin the help of the muscles is no longer the same. and the more so as sensation is there less acute. In the deep organs sensibility is still more obtuse, although it is still present ; and hence, this weakened sensibility is little known to us. We may make an exception as regards the muscular tissue, in which the relations between sensation and motion once more become evident ; but in approaching this aspect of the question we enter into the detail of the function instead of considering it as a whole. We may, to begin with, confine our study to that of touch properly so called, and to the motor reactions by which it is directly served.

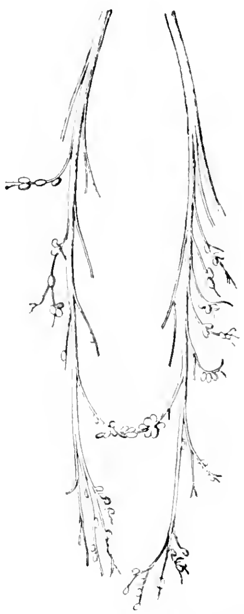


FIG. 207.—Pacinian corpuscles of the middle finger (after Henle and Kölliker).

A. DATA FURNISHED BY ANATOMY.—The organ of touch, properly so called, extends over the whole surface of the body with the *skin*, which contains its special apparatus.

Cutaneous covering.—These apparatus, which sometimes go by the name of teminations of sensory nerves, are, on the contrary, their origin, if we consider these nerves no longer from the point of view of their development, but only as paths of conduction. They differ in their structure and their situation. In fact, anatomists distinguish between sub-dermic apparatus, intra-dermic apparatus, and intra-epidermic nervous ramifications, to which is commonly conceded the function of being receptive for cutaneous impressions.

Sub-dermic apparatus.—Corpuscles of Pacini or of Vater.—These are ovoid bodies, visible to the naked eye, but more clearly with the lens (they are from 1–5 millimetres long), divided at the extremity into nervous ramifications, situated in the subcutaneous cellular tissue. They are formed of a thick covering made up of a series of very regular concentric layers (the last expansion of the

sheath of Henle). A nerve fibre, soon despoiled of its myelin, and reduced to its axis cylinder, penetrates into the cavity, traverses its long axis, afterwards displaying several short ramifications which assume the shape of a button. Between the fibre and the capsule a cellular mass is interposed (the club) formed of special cells.

Distribution.—These corpuscles are unequally divided according to the cutaneous areas. Rauber has counted on one half of the body—

On the shoulder	12	On the hip	5
On the forearm and the arm	161	On the leg and the thigh	138
On the hand	414	On the foot	275
On half of the trunk	46		
TOTAL	1,051 for half of the cutaneous surface.		

They are found not only under the skin, but also in the articulations, the bones and the mesentery.

They are not the organs of touch, but those of a more general function of sensibility than that we call tactile.

Intra-dermic apparatus.—Corpuscles of Meissner.—Much smaller than the preceding, these are olive-shaped and are deprived of the thick covering possessed by the former. The nerve fibre which penetrates them, instead of being straight, makes more or less numerous spiral turns. It gives off axis-cylinder ramifications deprived of myelin towards their extremities, which in this corpuscle are arranged in a regular manner. This corpuscle is, in fact, formed of special cells,

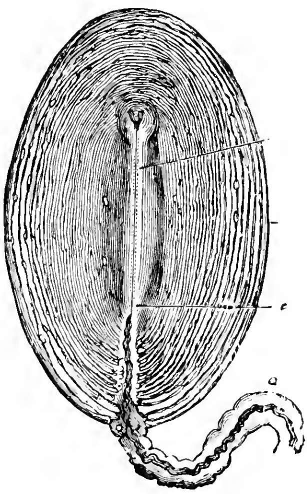


FIG. 208.—Pacinian corpuscle of the mesentery of a cat (after Frey).

a, nerve fibre forming its pedicle; *b*, system of lamellæ or concentric capsules; *cc*, central cavity where the axis cylinder is found.

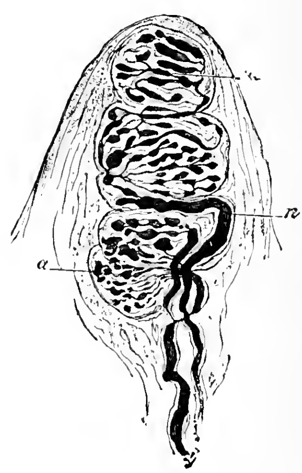


FIG. 209.—Papilla of the skin of the forefinger with a touch corpuscle (after Ranvier).

nn, afferent nerve tube: *aa* glomeruli with their tactile discs (prepared by the chloride of gold method).

which may be called specific, since they transmit the impulse to the polar ramifications of the sensory nerve. And for this purpose each ramification with its swollen or flattened extremity is included in the interval between two cells. Thus the number of these cells is proportional to that of the ramifications. These corpuscles are simple or composite, according to whether the fibre ending in

them remains simple or is divided for the purpose of distributing its ramifications to several superposed formations.

Distribution.—The corpuscles of Meissner have a much more restricted and much better defined localization than those of Pacini ; their seat is in the hand and the foot, specially in the pulp of the fingers and the toes. They are more closely allied than are the preceding to the function of touch properly so called.

In different areas endowed with a fairly large amount of sensibility may be found analogous but simpler formations: for example : the corpuscles of Krause, in the conjunctiva, which seem to be a rough sketch of the preceding : the spiral twists are scarcely indicated, and the tactile cells are reduced to a very small number—three or five.

Intra-epidermic ramifications.—The epidermis is penetrated by uncovered arborizations, springing from the network of the nerves of the cutis vera, which plunge into its thickness and penetrate right into the cell of the mucous bodies of Malpighi, in which they terminate. The relations of the cutaneous nerves with these cells (which are of an epithelial nature) immediately recall those of these same nerves with the cells of the glands of the skin and also the nervous glandular terminations in general.

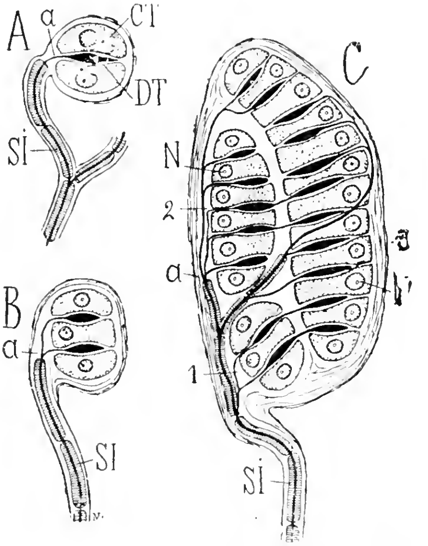


FIG. 210.—Tactile corpuscles of increasing complication (after M. Duval).

A, corpuscle of Grandry with one tactile disc DT, and two tactile cells CT ; B, corpuscle with two discs and three cells ; C, corpuscle of Meissner ; 1, 2, 3, its components (corpuscles of Grandry) ; N, nuclei of the tactile cells ; *a*, nerve fibre ; SI, interannular segment.

Up to the present time there has been no hesitation in comparing them to the receptive arborizations of the nerves of sensation ; and this opinion is founded on the belief that the epidermis, in which no appreciable movement can be discerned, has no connexion with the centrifugal nerves. This purely negative opinion may be devoid of foundation. The fact of the penetration of intra-epidermic nervous terminations into the protoplasm of the investing cells of the skin would lead us to suppose that the nerve conveys the impulse to these cells rather than that it receives it from them. These terminations are probably, in part, those of the centrifugal elements, which have been discovered in the posterior roots.

Deep organs.—Not only the skin, but also the deeply seated organs, the mucous and the serous membranes, in fact all the organs possess sensory nerves, of which the initial arborizations insinuate themselves between their elements or component bundles. The mesentery contains corpuscles of Pacini in the conjunctive tissue which separates its sheets. These same corpuscles may also be found in the connective tissue which borders upon the articulations. The capillaries display terminations which are supposed to have a sensory function (Ranvier). The dura-mater contains nervous ramifications with free arborizations (P. Jacques). The muscles and the tendons are also provided with sensory receptive organs, of which mention will be made when alluding to the muscular sense. This is an

extension to most organs of a variety of sensation analogous to that of the skin, this being what has gained for it the name of *general* sensation, and not the demonstrably incorrect fact that it is an element common to all other sensibilities. It is of a *special* nature, but its anatomical field has invaded nearly all the organism, with the exception of some restricted areas.

B. Data of physiological observation.—We need only observe our own organization to be convinced that impressions received by the cutaneous surface arouse in us sensations of varied nature. There are generally discerned : (1) the sensation of *contact* (touch properly so called) ; (2) the sensation of *temperature*, which may be divided into a sensation of *heat* and a sensation of *cold* ; (3) the sensation of *pain*.

This distinction is especially based on the fact that each of these three modalities of cutaneous sensibility may disappear in an isolated fashion, allowing of the persistence of the other two ; thus arise the three varieties of sensory cutaneous paralysis, *anæsthesia* properly so called, *thermo-anæsthesia* and *analgesia*.

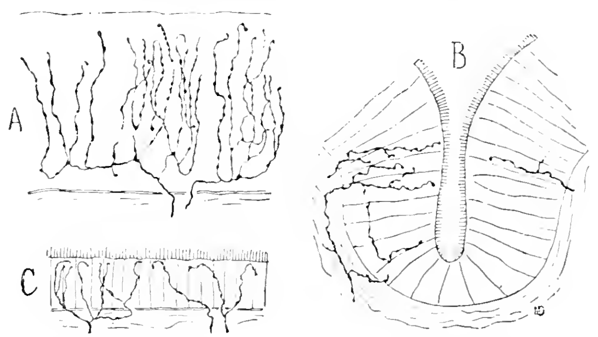


Fig. 211.—Various intra-epithelial terminations.
A, epithelium of the larynx (vocal cords) ; BC, respiratory region of the nasal fossæ with its vibratile epithelium, in the rat.

The problem here laid down is to ascertain if these three very distinct forms of cutaneous sensibility are, when starting from the place where the reception of impulses is effected, united to special receptive apparatus and to distinct conductors, or if their modality depends on distinct conditions of the functional activity of common apparatus and conductors.

1. **Nature of the stimuli.**—Starting from the stimulus itself, we see that it is presented under two forms (and not three), which are clearly distinct : first, a stimulus of a *mechanical* nature, which is the contact of bodies with the skin, and which when exaggerated becomes pressure ; and second, a stimulus of a physical nature, heat, which we compare, not to a massive, but to a *molecular* movement of warm bodies. *Pain* has no special stimulus ; *it generally arises whenever the stimulus acquires an exaggerated intensity*, which, exceeding the usual limits of the function of organs, exerts in consequence a more or less destructive action on these organs.

It is maintained that this is the case not only as regards the skin, but also as concerns the sensorial apparatus with more or less precision : too brilliant a light, too acute or too shrill a noise give rise to a *disagreeable* sensation, which is pain in an attenuated form.

Discussion.—This first distinction being made, we may inquire if the specificity of the two remaining stimuli is connected with the specificity of the apparatus receiving their exciting shocks. In organs like the eye or the ear, the question is easily answered, because the specific receptive elements are distinct, both as regards form and their special situation in the interior of the apparatus. In the skin, supposing that such elements exist there, these two characters would be wanting : there are no cutaneous areas especially appropriated for the reception of thermic impressions, as the retina is in the eye for that of luminous impressions, amongst other membranes possessing a common sensibility : and although we find in the cutaneous covering as many as three orders of apparatus receptive of stimuli, yet we have no reason to believe that any of them is specifically connected with the sense of temperature. As, on the other hand, the specificity of thermic sensation is evident, we find ourselves confronted by a problem the solution of which requires a certain amount of information which is now lacking.

While on this subject it may be added, that the specific receptive element of any particular sense may be brought into play by stimuli of different nature. The retina, for instance, is specifically excitable by the ethereal waves which we call luminous, but it is so also by mechanical means, the phosphenes being a proof of this. Spread out on the surface of the skin instead of being sunk behind the refracting media of the eye, the retina would warn us at the same time of the contact of bodies and of the existence of luminous waves. It is true that it would only give us a solitary and unique impression analogous to that of the phosphenes. In fact, far from going out to seek mechanical stimulation from the contact of bodies, the retina is, on the contrary, protected from it by its position located deeply behind the transparent media, which only allow of its being reached by undulations of the ether ; this prevents it from learning how to differentiate between the two stimuli. If these conditions were altered, it might be possible for it to become capable of furnishing us with the elements of the two sensations. It is necessary to seek in some condition of this nature for the capacity of the skin to give us information with regard to excitations, both thermic and mechanical.

2. **Experimental dissociation.**—The different sensibilities of a cutaneous area may be observed to be dissociated after injuries or operations affecting the corresponding sensory nerve. After section of a nerve trunk it has been found that the thermic and painful sensibilities have been lost, while tactile sensibility has been preserved (Létiévant, Weir-Mitchell, Richet, Charcot, etc.) ; or, rather, they are all three abolished, but the area of thermic, and painful insensibility markedly encroaches on the area of tactile insensibility (Cavazzani, Manca). This dissociation is called *syringomyelic*, because it is observed in certain affections of the spinal cord. If a superficial nerve like the ulnar is compressed, the different sensibilities will also be seen to progressively

weaken and disappear; the thermic and that of pain first, while the tactile sense is relatively preserved (Biernacki).

Facts of this nature seem, at first sight, favourable to the existence of distinct conductors for these different modes of sensation. At the same time, even from this simple point of view, the difficulties of the interpretation are not avoided, and the following hypothesis may be preferred to it. Each sensory nerve has its area of distribution in the skin, but these areas mutually overlap. The persistence of tactile sensibility after section of a nerve trunk may be explained by the fact of the invasion of its territory by the fibres of the neighbouring trunks. The weakening or abolition of thermic and painful sensibility may be explained by the insufficiency of this collateral innervation. In other words, stimulation, in order to produce pain or the sensation of temperature, must affect more fibres in the same point than it is necessary for it to do in order to produce the sensation of contact.

3. **Persistence of the impression.**—It may be demonstrated (both for the skin and the retina) that the impression persists a certain time after the removal of the stimulus. If, by the aid of a rotatory mechanism, two shocks are periodically communicated to a finger, being repeated on the average at $\frac{1}{45}$ of a second interval, these two impressions are perceived as one. If the two successive shocks are received by two symmetrical fingers on the two hands, the result is the same. This is a proof that the sensation of the first shock still lasts, with a practically uniform intensity, until the arrival of the second impression. The rate of the shock augments the persistency of the sensation, but in a feeble manner.

Estimation of the rate of transmission in the sensory nerves.—On this fact a method of measuring the rate of nervous transmission in the sensory system has been founded. If, instead of receiving the two shocks on two symmetrical regions, that is to say, on two regions placed at the same distance from the brain, the second shock is received in a region nearer to the latter: for example, the hand and the face, a fusion of the sensations results, but leaving a greater interval than when the two symmetrical regions were in question. The difference between the two intervals measures the difference of duration between the two transmissions. On the contrary, if the shocks are received, the first on a finger and the second on a toe, the interval in order to obtain fusion must be diminished by the entire quantity representing the difference of duration of the sensory transmissions from the foot and the hand respectively up to the sensorium. According to these experiments, the rate of transmission is greater in the spinal cord than in the nerves (Bloch).

4. **Primitive element of tactile sensation.**—According to Mendelssohn, every sensation elicited by mechanical irritation of the skin may be reduced to a sensation of pressure: if this is not the only element of tactile sensation, it is at any rate its principal element. The sensation of pressure varies according to two conditions, two factors, which are, first, the *intensity* of the stimulus or weight supported, and secondly, the *extent* of the cutaneous surface submitted

to the pressure. By varying individually either one or the other of these factors, two series of values are obtained.

If, on an equal surface, the intensity of the weight is varied, the *differential perceptibility* of the direction of the pressure is determined.

If, with an equal intensity of stimulus (with equal weight), the stimulated surface is varied, the *tactile acuteness* is determined. This plays as regards the tactile sense the same part that visual acuteness plays in that of vision.

Differentiated perceptibility and tactile acuteness are necessarily closely connected with each other, the first being unable to operate without the second. Nevertheless, they are susceptible of undergoing independent, but not parallel, mutual variations when cutaneous sensibility varies (according to the area, the state of the subject, and lesions of the nervous system).

5. **Stereognostic sense.**—We possess the faculty of appreciating with *the eyes shut* the form of bodies brought into contact with the skin. This appreciation is, however, only approximately accurate as regards the most sensitive surfaces, the palm of the hand for instance; it brings two factors at the least into play, namely, on the one hand the tactile sensibility of the cutaneous area in contact with the object sought to be recognized: on the other hand, the deep sensibility of the parts which either undergo or execute, the movements of the hands and fingers ensuring their contact with the object. A portion of this sensibility returns to the muscles which execute these movements, and is allied to the so-called *muscular sense*.

Thus we see that, when the sense of touch is exercised, an active element intervenes to amplify and complete the information provided to us by this sense, whence is derived the name *active touch* given to it under these circumstances.

Stereognostic sensation is a complex sensation.—It is formed by the association of simpler sensations and is developed in a more complex system than those serving alone as a field to these last-named.

A. PROJECTION ON THE GREY AXIS

The tactile stimuli received in the cutaneous nervous apparatus are projected into the spinal cord. This projection is effected by the paths of the neurons of the posterior roots. For each of them it is merely an ordinary and isolated fact of conduction. But it is remarkable that even from its origin, that is to say, from the apparatus receptive of the stimulus, this projection implies the fact of association. We know that each sensory root has a determinate cutaneous area; but we also know that these areas mutually penetrate to such an

extent indeed that the area of a given root is covered in its superior half by that of the root of the preceding number, and in its inferior half by that of the root of the following number. An area of the skin of such small extent as only to give *one* sensation to the compass of Weber, in reality projects the stimulus by *two* or *several* roots. Unity of sensation is in no way incompatible, as is obvious, with multiplicity of conducting tracts. The *impulse*, even before reaching the grey matter of the spinal cord, falls into a systematized assemblage which helps to diffuse it throughout the nervous system.

1. **Passage through the spinal ganglia.**—The ganglia of the posterior roots contain the cells of origin of the neurons of projection between the skin and the spinal cord (sensory nerves), cells which may be considered as being placed on their course at a great distance from their two extremities. These cells were at first thought to be mutually unconnected, following the example of the nerve fibres. Dogiel has since shown that they are provided with prolongations, by means of which the radicular posterior neurons can enter into functional relationship with each other, either directly or by the intervention of short cells of association whose ramifications, both those of the dendrites and of the axis cylinders, do not transgress the boundaries of the ganglion. These prolongations of the radicular cells would further provide them with connexions (still, however, rather ill defined) with the great sympathetic.

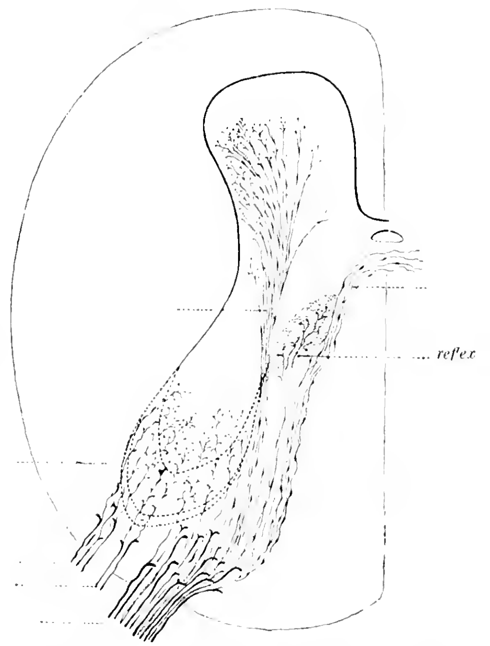


FIG. 212.—Collaterals of the posterior roots.

Diagram of groups of posterior roots giving off their short, medium and long collaterals at their entrance into the spinal cord (Charpy).

The spinal ganglia thus resemble the spinal cord in structure, and they are in fact a portion of the cord embryologically diverted, and therefore possess its functions in some degree. I have tried experimentally to ascertain if it might

still be possible to find some indication of the obvious transformatory action possessed by the spinal cord on the impulses which traverse it; and with this end in view have studied the characters presented by the reflex responses to stimuli brought to bear on the sensory nerve *before* and *after* their passage through the spinal ganglion. I was unable to discern any certain modification in the most prominent features of the reflex movements thus obtained. Either the characters under observation (latent period, fusion of impulses) are not those which depend on ganglionic action, or else, in comparison with those produced through the agency of the spinal cord, these modifications are too feeble to obviously appear in the tracings of muscular movement studied in this double condition.

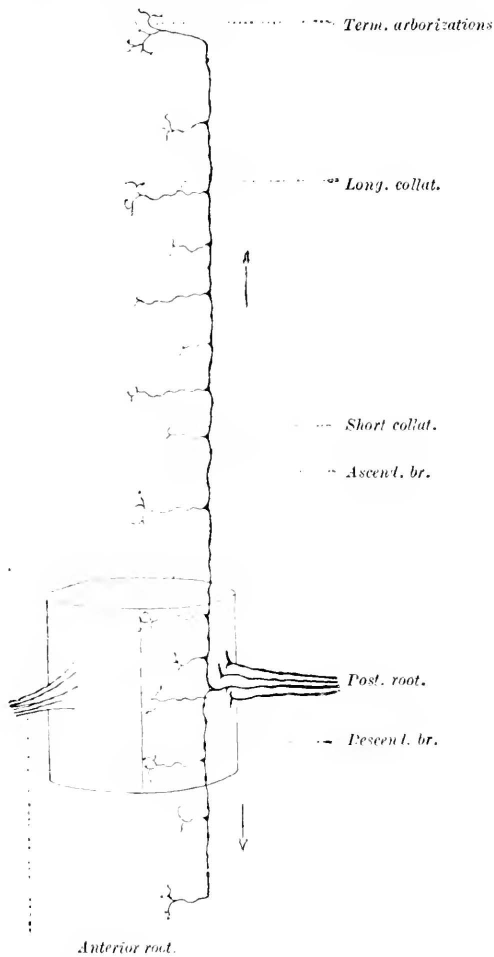


FIG. 213.—Posterior root with its ascending and descending branches and their collateral and terminal ramifications.

Dispersion of the impulse over a large extent of the grey axis.

2. **The posterior radicular fibres.**—The posterior radicular fibres, on penetrating the spinal cord, are arranged in two groups, of which the one is *external* and the other *internal*, these groups differing by the thickness of their fibres and the length of the course which they run in the spinal cord before going to rejoin the various areas of the grey matter.

The type of their connexions is not essentially different in the short, medium, or long fibres. These last form the group which is called internal or *median*. The variations in the structural type must correspond to functional modalities, of the nature of which we are ignorant.

When studying the function of the elements of the spinal cord, we had occasion to speak of the sensory roots and their principal connexions.

A fact which we owe to the application of the new anatomical methods, and which will at first sight cause surprise, is *the extraordinarily extended development*

of the polar field of distribution of the posterior radicular neurons considered individually (principally the internal group). Some of these extend the whole length of the spinal cord, and even beyond, in order to reach the inferior nuclei of the medulla oblongata, or perhaps the cerebellum. And what will also cause astonishment are *the number and varied connexions of the ramifications of this field of distribution with the grey matter of the spinal cord,* so that the principal regions of the grey matter receive the expansions of the same polar field.

At its entrance into the spinal cord the posterior radicular fibre is divided into two branches, one *descending*, shorter (but which, nevertheless, may in some cases attain more than 5 to 7 centimetres) : the other *ascending*, whose terminal extremity attains the nuclei of Goll and of Burdach in the inferior part of the medulla oblongata. These branches give off *collaterals*, themselves subdivisible into *short*, which are lost in the posterior horn (substance of Rolando) ; *medium*, which go to the column of Clarke (a small number pass through the posterior grey commissure and form a commissural tract) ; *long*, which run to the anterior horn of the same side (these last arise near the bifurcation, and consequently near to the root which has produced them, and hardly leave the same medullary segment).

3. **Dispersion of the stimulus.**—The nuclei of Goll and of Burdach are the principal origins of the fillet (ruban de Reil), or sensory medullo-cortical tract ; the column of Clarke is that of the direct cerebellar tract ; and the anterior horns of the spinal cord that of the motor roots. The impulse is therefore conveyed to tracts which disperse it in three directions as divergent and remote as possible, namely, towards the *cerebral cortex*, towards the *cerebellum* and towards the *muscles*, these being the immediate organs of movement. Further, this same grey matter offers it the dendrites or receptive poles of numerous neurons, whose fibres are both direct and crossed ; some of these, long, like those of the tract of Gowers, ascend to the cortex or the cerebellum ; others, medium, unite the stages of the spinal cord which are more or less distant from one another ; and still others, short, associate the elements which are near to each other in the same limited area of the spinal cord for the discharge of extremely varied functions.

The dispersion of the impulse in so many and such varied directions, these themselves being in connexion with tracts of contrary direction, which concentrate it on the organs executing the functions, would engender the most inextricable disorder in these functions, were not the impulse itself governed by laws whose effect we can observe, but whose principle is unknown to us. Sometimes the impulse overflows to the brain, and seems to exhaust itself in sensory or psychic effects without any immediate motor results ; at other times it does not end in the consciousness, but without delay gives rise to movement. Between these two extremes there is room for the most varied gradations and combinations. Anatomy has done the very great service of showing us the tracts in which it is possible for the impulse to become in-

volved, in order that it may realize acts as diverse and as contingent as those which we execute both internally and externally. For the verification of this purely static state, we are not in a position to superpose the dynamic conditions answering to each of the changes of which some alone are visibly and externally revealed to our eyes.

Function of direction or of shifting of the points (*aiguillage*).—The obvious conception of these changes implies, as regards some of them, the existence in the nervous system of a function of direction or of shifting of the points, to employ a comparison which exactly expresses, but in metaphorical terms, the idea required. We may admit this in principle; only, with regard to the mechanism of this function, as well as the conditions which determine its execution, positive facts are at present altogether lacking.

The determining conditions of this phenomenon of direction are not all in relation to the actual stimulus (nature, form, intensity); some of them are internal to the nervous system (at the moment when it receives the stimulus); and these conditions seem to be of the same nature as those which take part in the phenomenon of *attention*.

4. **Short circuit; reflex action.**—When the impulse brought by the long collaterals to the motor nuclei of the anterior horn finds a road for going to the muscles, it accomplishes one of the shortest and most simple journeys that it can perform in the nervous system. The name of *reflex collaterals* has been given to those terminations of the posterior radicular neurons, which, speaking generally, associate the two corresponding roots of a nerve pair for the performance of a sensori-motor act of the most simple form. That the impulse really follows this route may be demonstrated by isolating the metameric segment corresponding to the nerve pair from the rest of the spinal cord by

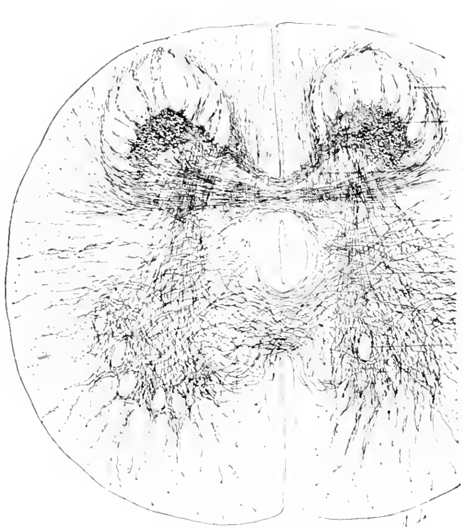


FIG. 214.—Collateral fibres of the spinal cord (after Cajal).
Collaterals of the columns and of the roots seen in a transverse section of the thoracic spinal cord. New-born dog (method of Golgi).

means of a double section made above and below it. But it must not be imagined that these collaterals are the only reflex paths ; all the other ramifications, both collateral and terminal, of the posterior radicular neuron may involve the impulse in circuits which, though more unequal, are none the less reflex circuits.

The expression " reflex act " is generally synonymous with an unconscious-voluntary act. With regard to this, it must not be forgotten that the participation of the brain and of the cortex by no means necessarily implies a conscious element in the sensory and voluntary manifestation of the motor phenomenon. There are reflex actions which have their seat in the cortex. The depth of its penetration is not the only, or the determining, condition for the appearance of consciousness : the association of different cortical areas, on the contrary, plays here a part of the first importance.

From the rudimentary sensori-motor phenomenon which operates in the isolated medullary segment, up to the phenomenon of ideation which correlates the different sensorial systems with their motor dependencies, the gradation is progressive and uninterrupted.

5. **Long circuit ; conscious action.**—When stimulation terminates in a conscious phenomenon, in sensation, the latter, as already mentioned, may present three modalities. It may be a sensation of contact (*æsthesia*), a sensation of temperature (*thermo-æsthesia*), or a sensation of pain (*algesia*). So far as concerns the primary paths of the system (radicular elements), the localization of the stimuli giving rise to these three sensations into three orders of conductors distinct the one from the other has been given up. But, starting from the grey medullary matter, and considering the somewhat decided morphological differences of the fasciculations which prolong the system towards the encephalon, it has often been hoped that a distinct functional action for each of these might be found, by appropriating it to the isolated transmission of one or the other of these sensory modalities. And not only the tracts, but also the grey matter has been compared to a conductor, and the question has been mooted as to the conducting attributes of the grey matter, compared with those of the tracts.

Syringomyelic dissociation of the different sensations.—The most cogent argument that can be brought forward in favour of the specific conduction of each of the sensations arising in the skin is the dissociation which they undergo from the presence of certain changes affecting the spinal cord in *syringomyelia*.

This is a disease of the spinal cord in which *disappearance of sensibility to pain and temperature may be observed, tactile sensibility being retained.* The lesion which causes the dissociation is a gliomatous

degeneration which, invading the grey matter, destroys it for a certain length, replacing it by *cavities*, but which does not interfere with the white matter.

6. **Localizing hypothesis.**—This is the reproduction in human beings of an experiment of Schiff, which consists in cutting away (as far as possible) the grey matter, while respecting the continuity of the posterior columns. The result would be the same in both cases: abolition of certain kinds of sensation and retention of others. In the dog thus operated on, tactile sensibility persists, while that to pain is lost. Hence it has been concluded that the posterior columns are those which convey tactile impulses (Schiff), while the grey matter would be the path for impressions of sensibility to pain (Brown-Séquard).

Criticism.—This view was for some time very favourably regarded. Clinicians found in the experiment of Schiff a solid basis for the interpretation of the symptoms of syringomyelic dissociation, and physiologists, for their part, found in the clinical facts and those of pathological anatomy, a support for conclusions which were not in themselves obvious. Unfortunately, a somewhat rigorous criticism of these facts allows hardly anything to remain of the fundamental hypothesis. Clinical observations indisputably confirm the fact of the dissociation of sensibility to pain, to temperature, to contact, one may indeed add, to pressure, to heat, to cold; in a word, to all the known varieties of sensation. The separation, it is true, is not always complete; but in most cases it is extremely distinct. Only, the order according to which these various modalities of feeling group themselves or disappear is not always the same; it is sometimes the reverse of what we have above said; in that case it would be tactile sensibility which would be involved, without any change in the sensibility to pain or to pressure. Further, the sensibility to cold may be preserved, and that to heat destroyed.

Discordance between symptoms and lesions.—If to each variety of dissociation a particular form of lesion of the spinal cord should correspond, nothing would be more valuable than the information thus furnished by pathology. Unfortunately, if the varieties of gliomatous degeneration differ amongst themselves, up to the present time no certain agreement between their variations and those of the clinical symptomatology has been observed. The law connecting the one with the other has not been determined; this law is therefore not that which would *localize* the different orders of sensibility in dissociated conductors, and to effect this would liken the grey matter to a conductor.[1]

The results obtained by Schiff in the experiment in question are not such as can be admitted without discussion. Philippeaux and Vulpian declare that they have seen nothing of the kind. Not that the possibility of these results can be denied. They may be produced by experiments on animals, in the same

[1] Syringomyelia (spinal cord assuming the form of a pipe) is due to a development of the cells or neuroglia of the grey matter, which atrophies and disappears, leaving cavities, or even a single cavity extending the whole length of the spinal cord. Sometimes the lesion respects a portion of the grey matter, sometimes it also invades the white matter. In both cases it more or less compresses the latter. It is maintained, but without very clear proof, that the posterior columns suffer less than the others from this compression.

way as disease produces them in man ; but the conditions ensuring their constancy are not exactly determined in either case.

Equivocal formula.—If it be conceded that the conditions are those indicated above, the formula indicating them is badly expressed. It places in opposition to each other the grey matter and the white matter of the spinal cord, as if tactile impressions had only to do with the first and painful impressions with the second. In reality both of these penetrate into the spinal cord by posterior radicular elements, which form part of its white matter, and by these are necessarily transmitted to its grey matter.

But this transmission is effected, as we have seen, in very different localities from this last-named ; certain collaterals reach the grey axis even in the prolongation of the roots, while others reach it higher up, and finally the terminal branches only at the level of the bulb.

The localizing theory of Schiff and Brown-Séquard presupposes that impressions of pain find in the grey matter, with regard to the roots which convey the impulse, or in their more or less immediate neighbourhood, a path of transmission to the brain, and that the tactile impressions do not follow this route ; conversely, it assumes that tactile impressions find their path of transmission in the bulbar nuclei or in their neighbourhood, and that impressions of pain do not. The interruption of the grey matter between the level of the root under consideration and the bulbar region will therefore suppress the conduction of painful impressions *after* their penetration into the grey axis, but will permit of the penetration of tactile impressions. Section of the posterior columns at the same level will suppress the conduction of tactile impressions *before* their penetration into the grey axis, but will leave the field open to impressions of pain ; all this being based on the hypothesis of their localization in distinct conductors from the spinal cord up to the brain, a hypothesis which we reject.

7. **Bulbar reflexes.**—On account of the prodigious extension of the polar fields of the posterior roots, the impulse conveyed by the latter undergoes a first dispersion ; the grey medullary matter, by means of the fibres, both of projection and of association arising from it and which follow such very different directions, causes it to undergo a second dispersion. We have seen that a choice is offered it by the grey matter between the motor nerves which pass it on directly to the muscles, or the encephalon which exerts upon it a power of conservation, and we know that between these opposite limits it has other localities for transformation and for reflexion open to it. The medulla oblongata is one of the most important of these. Rosenthal describes it as taking part in a great number of reflex actions which it has been the custom to regard as being purely medullary. This intervention is particularly observable in the reflex acts which react on the great sympathetic (vaso-motor, secretory, vaso-dilator actions, etc.).

Experiment.—If a sensory nerve like the sciatic or any other nerve trunk of the same function is stimulated, this stimulation, in addition to the internal or purely psychic phenomenon of pain, gives rise to a large number of reflex manifestations, both as regards the muscles of the skeleton, including those of respiration, and the organs discharging

nutritive functions. In order to appreciate them better it is necessary to dissociate them. The most prominent of these manifestations are suppressed by placing the animal under the influence of curare, which paralyses the voluntary nerves and those of respiration. Should then a phenomenon of painful sensibility be provoked, it is noticed that the heart's action is slackened (sometimes it may even be stopped); in a large number of organs, but especially in the viscera, the arterial capillaries contract and cause the general arterial pressure to rise; at the same time the cutaneous capillaries are dilated, and congest the circulation in the superficial regions; the pupil is dilated; the cutaneous glands secrete, etc. If the bulb is separated from the spinal cord by section, the stimulation no longer has the same effect. If, after a certain interval, the experiment is recommenced, it will be seen that the effects reappear, but are less marked. This is a proof that, as concerns all these actions of organic life, the medulla oblongata is an important centre of reflexion, but that it is nevertheless, not the only one, although its action in this respect predominates greatly over that of the spinal cord.

B. TATICLE CORTICAL AREA

The impulses received from the surface of the skin do not all reach the cerebral cortex; a large number of them are dispersed or reflected at variable altitudes, from the spinal cord in passing through the cerebellum and the cerebral ganglia. Those which, after numerous transformations in the subjacent layers of the grey matter, reach the cortex, there give rise to the phenomenon of *tactile sensation* called *general sensibility*, in opposition to the other sensations which arise from impressions of a different nature, collected on more limited surfaces (special sensations).

1. **Cortical localization of sensation.**—It is maintained that tactile sensation is developed in a limited and determinate area of the cerebral cortex; which is as much as to say that, after the destruction of this cortical area, the clear, distinctly conscious sensation of touch will no longer be present. If the injury should affect one of the two hemispheres, there will be anæsthesia of one of the two sides of the body; should both the hemispheres be injured, the *anæsthesia* will be generalized.

The delimitation of the tactile cortical area (tactile sphere of Munck, centre of tactile sensation of many authors) has given rise to much discussion. For reasons somewhat theoretical, it was at first located in the posterior part of the

brain behind the excitable motor area (doubtless by analogy with what is observed in the spinal cord). Facts, both clinical and experimental, compelled the abandonment of this theory, and the area of tactile sensation is now known to be confounded with the motor area itself; or, to put it otherwise, is located in the central convolutions situated in the immediate neighbourhood of the fissure of Rolando.

Sensori-motor area.—The clinical facts on which this localization has been founded are due more especially to the researches of R. Tripier (1880). From the first, and in spite of the predominance of a contrary view, this observer has held that motor paralyses (hemiplegias), caused by a destruction of the Rolandic area, are constantly accompanied with a diminution of sensation: this hypoæsthesia being, not the

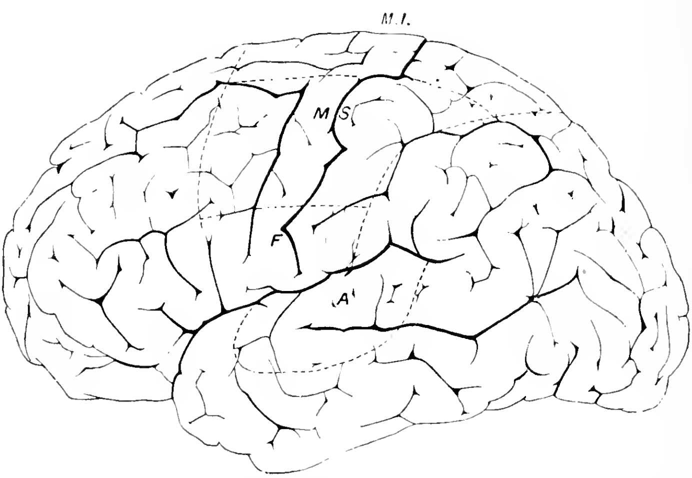


FIG. 215.—Sensori-motor and sensorial areas of the external surface of the hemisphere.
Sensori-motor tactile area subdivided into three regions.
MI, area for the inferior limb; MS, area for the superior limb; F, area for the face; AC, sensorial area of audition (after Dejerine).

exception, but the rule. *The motor area is in reality a sensori-motor area.* Physiological facts, after the most careful examination, point, as Luciani and Munck have found, in the same direction. The destruction of the motor area is followed by effects recognizable, not only in the domain of *motricity*, but also in that of *sensibility*; it must, however, be borne in mind, that the expressions *motricity* and *sensibility* have a meaning which is sometimes extended to every production of movement and to every phenomenon of reaction against external stimulation; this acceptation may sometimes, on the contrary, be limited to certain modalities of movement or of the reaction which reveals sensibility to us.

The destruction of the motor area in an animal allows of the persistence of a large number of movements of very varied functional modality; some of these movements are simple, and others complicated; all, however, are co-ordinated and adapted to a given end. Even motor spontaneity does not seem to have disappeared, which fact proves that the sources of stimulation have remained numerous and of varied character; but certain modalities of movement (especially that executed by the limbs) have disappeared for ever, and the

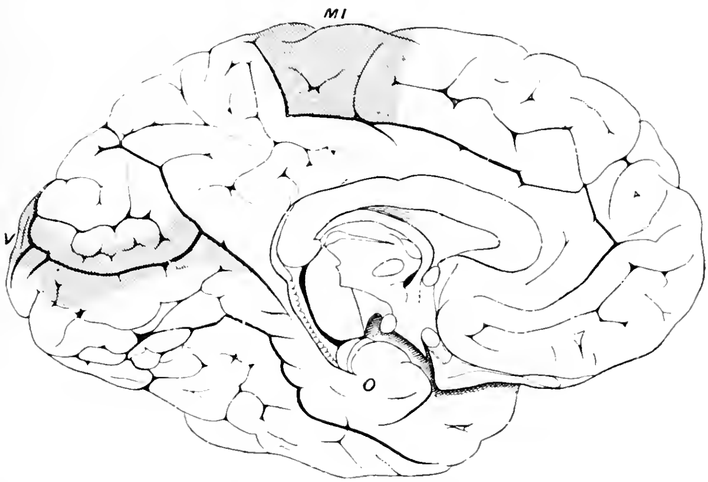


FIG. 216.—Sensori-motor and sensorial areas of the mesial surface of the hemisphere.
MI, paracentral lobule forming part of the sensori-motor tactile area.
V, visual area; O, olfactory area (after Dejerine).

corresponding motor paralysis will only appear after search for these movements amongst others more or less resembling them.

The destruction of the so-called motor area, which we describe with Tripier as sensori-motor, also allows of the continuance of a certain number of defensive or responsive movements on the part of the animal, these being often considered as evidence of sensibility; but, as the author just mentioned has observed, it will suppress a certain number which will never reappear, both in the dog and in man. It is for these that search should be made if it be desired to recognize and define the sensory paralysis following the cortical lesion thus produced.

Progressive differentiation in the series.—The sensori-motor phenomena depending on the sensorial areas in general, and on the tactile area in particular, have an importance, and a distinct physiognomy all the greater in proportion as to whether, in any given individual, they correspond to a more differentiated and more frequently exercised function. It is only under these conditions that

the deficiency will appear permanently, in the domain both of motricity and of sensibility. It will be much more apparent in man than in the monkey, and in the monkey than in the dog; below the latter, it is hardly worth while seeking it in the case of lesions limited to a circumscribed area of the cortex. It will appear in man much more obviously in the arm than in the leg, and in the hand and the fingers much more than in the other segments. In animals, also, it must be sought in the extremities (Mott).

Functional balance.—This is one of the examples of the law to which we have already had occasion to allude. The cerebral functions, those which create animality, and above that again, humanity, are nothing but the primordial functions of the nervous system, slowly, but progressively and deeply, differentiated: in the same way that the brain, which, to begin with, was only some sort of a segment of the nervous axis, has assumed an adaptation, a development and special connexions, to prepare it for the directive rôle which it should assume in the superior species.

The ganglia of the great sympathetic, the segments of the spinal cord, have remained as evidence of the primitive organization. In spite of being penetrated and invaded in every layer by bundles of projection which bring them into individual subjection to the superior segment, now become the brain, these organs still preserve traces of their independence and also of their federation. But their autonomy (both individual and collective) has been much diminished even here, and has given way to a more pronounced *centralization*. This is why the functional deficiency following the destruction of the cerebral cortex in the superior species, and especially in man, is so pronounced.

The functional substitutions, which are easily effected between similar organs, or those only slightly different, become impossible between organs which have undergone a double inverse evolution (retrogressive for some, progressive for others) which has thus profoundly differentiated them. It may be added that this differentiation is of unequal value for the various cortical functions, and therefore for the diverse systems, areas and organs by which these functions are executed; this is what causes the unequal disturbances following lesions which seem equal or equivalent.

2. **Imperfect superposition of sensory and motor areas.**—If the cortical area of tactile sensibility is superposed to that of the so-called motor area of the brain, it is well to add that it is not superposed to it in an exact manner; or, to put it better, we have no absolutely certain criterion for tracing distinct limits around either one or the other of these territories. Further, we know that these limits do not exist in a sharply defined condition, but that they are formed by a continuous degradation. Apparently the sensory area extends far beyond the motor area. This seems, at all events, the conclusion which is deducible from the following observations: *for equal lesions the sensory paralysis is less evident and of less extent than is the corresponding motor paralysis;* it is also more transitory; and, after having been very distinct, it may to a large extent disappear.

Difficulties of comparison.—It must also be recognized that means of comparison are too often wanting. Like sensibility, motricity is of various kinds: according to the modality assumed, the motor

or sensory phenomena may be affected more or less gravely by the cerebral lesion, or be to a great extent respected by it. Speaking of sensibility alone, a difference must be drawn between *algesia* and *thermo-æsthesia*, which generally resist even extended lesions, and *touch* properly so called, which, other things being equal, is more compromised. Again, we must distinguish between the *sensation of contact* and that of *active touch*, or the faculty we possess of localizing objects, and of associating in the same representation muscular and tactile sensations. This last modality is the one which disappears most readily, and in the most persistent manner.

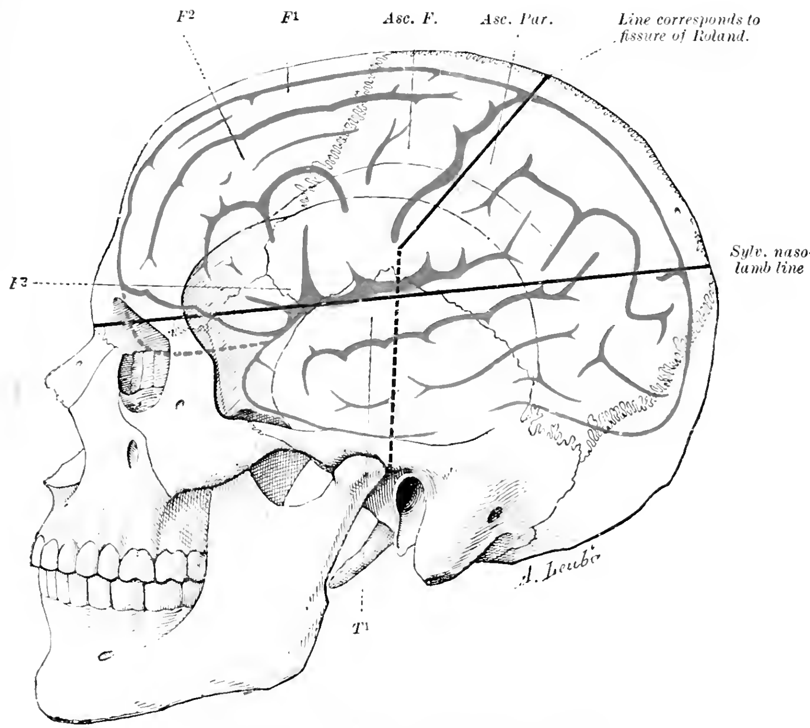


Fig. 217.—Cranio-cerebral topography.
Rolandic line and Sylvian line (after Poirier).

Data furnished by anatomy.—Again, the sensori-motor nature of the Rolandic area is demonstrated by anatomical data. The fillet (ruban de Reil), the prolongation in the brain of the sensory tracts of the spinal cord, spreads itself out in the central convolutions; this is demonstrated by the facts of embryology and the study of degenerations made both in man and in animals.

In reality the fillet is composed of two bundles arising, one in the grey matter of the spinal cord (lateral fillet), the other in the lower portion of the bulb in the nuclei of Goll and of Burdach (mesial fillet), which, on leaving this, are united together and then, following the crura cerebri and the internal capsule, proceed to the cortex. Flechsig has followed the former (lateral fillet) as far as the ascend-

ing parietal convolution and to some neighbouring areas. The second (mesial fillet) also joins the cortex in the central convolutions, but the larger part of its fibres are interrupted in the optic thalamus. From the bulb to the optic thalamus a *bulbo-thalamic* neuron extends, and from the optic thalamus to the cortex a *thalamo-cortical neuron*. Destruction of the central convolutions involves a retrograde degeneration of this second neuron, and an atrophy of the first without degeneration properly so called. However this may be, the tactile area is represented by a territory of the cortex which receives the terminations of the sensory paths (fillet, ruban de Reil) and the origins of the motor paths (pyramidal tract).

3. **Another localizing formula.**—When, according to facts furnished clinically and experimentally, the motor and the sensory areas were confounded in one single sensori-motor area, the hope was not on that account renounced of formulating a new theory which would reconcile with these facts the conception of a separate localization of sensibility and motricity. At one time it was thought to have been found in a division in depth of the so-called centres fulfilling one or the other function, the most superficial lesions of the cortex being those which are often accompanied with insensibility (Brissaud). Whether, with Golgi and Tamburini, motricity and sensibility be represented as cellular functions, or whether, with Flechsig, they be considered as functions of association, the conception which still predominates in many minds is that of a separate and, in some sort, absolute localization, and of a dissociation of the areas or fields of the two functions, one of these fields terminating at the precise limit where the other begins.

Critical examination.—I have already shown that this conception, which aims at the extension to the deep masses and to the cortex of the brain of the results of experiments made on nerve roots, is untenable. The radical distinction which, at the first glance, is seen to exist between movement and sensibility, should not lead us to ignore the necessary link which unites them. To less superficial examination this link declares itself under numerous aspects ; it exists both in the partial or general elements and systems as well as in the nervous system taken as a whole. In the cell, whether considered in an isolated manner or experimentally separated, this link is the basis of what we call its irritability. The cell responds by a movement to the stimulus coming from without, and thus reveals its state of irritation. In the nervous system and the large component systems resembling it this link is quite as important ; but, on account of the complexity of the systems involved, it allows of its principal methods of articulation being better seen. To my mind the error lies in considering this articulation as single and in locating it according to a plane of division (marked out in the cerebral cortex) which displaces the two phenomena,

the one in front, and the other behind it. The reciprocal penetration of the two phenomena is effected by roots which are prolonged in the two directions up to the confines of the nervous system. The cerebral cortex nevertheless remains the most remarkable locality of this system, but for reasons rather different to those which have been assigned. It does not contain in itself the boundary or surface of demarcation of sensory phenomena, but ought to be considered as the keystone of the systems giving to sensation its highest expression, which preserve it under the form of images, and finally attach it in time to the movements by which it always has to manifest itself.

If we imagine a section made with a sharp instrument following the ideal surface supposed to exist in the cortex between the sensory and motor field, we then, according to current ideas, should bring about in an effective and permanent manner this dissociation of sensibility and movement as it is usually conceived and as it is considered to exist at certain moments in the nervous system.[1] But such an operation (it is unnecessary to observe that it is wholly unrealizable) would not allow of the subsistence either of sensibility under the highly differentiated forms which are presided over by the cerebral cortex, or of movement under the equally superior form known as voluntary. In affirming this I use as a basis the conception which ought to be held of the partial systems composing the nervous system, inasmuch as these systems are self-sufficing and capable of an independent function.

Functional systems, their characteristic.—The assemblage of sensory roots is a systematization bringing near together elements of a definite type: the assemblage of the motor roots is the same. The first, surmounted by paths which prolong it up to the brain, or the second, surmounted by descending paths which proceed from the cortex, are more complicated systematizations than the preceding ones (they form what in other words is called the sensory and the motor field); but they are not yet systems in the proper sense of the word. On the other hand, a sensory root associated with a motor root in the execution of an elementary reflex action, represents a functionally definite system. That, then, which characterizes *a system* in the physiological sense of the word, is, on the one hand, *the association of sensibility with movement*, and, on the other, *the cyclic form*, which places the two phenomena in mutual dependence by causing them to succeed and engender each other reciprocally.

Typical form.—The reflex cycle is thus the prototype of the nervous organization and it is found from top to bottom of this organization. Functionally dissociated, the nervous system furnishes cycles of this kind both in its superior and in its inferior portions: some are simple and rudimentary; others are complex and formed by the association of the first; neither of them, however, is capable of isolated independent function, excepting in so far as it retains the cyclic form and organization, at least in a certain degree.

[1] It may, on the other hand, be observed that such a surface is not traceable in any manner, not even ideally, if it is intended to follow the articulations of the neurons (sensory on one hand, motor on the other) and at the same time to respect the continuity of the cerebral elements. It must, indeed, be remembered that the terminal poles of the one (axons of the fillet), and initial poles of the others (dendrites of the pyramidal tract), in addition to the contacts which enable them to transmit the impulse in a direct manner, are further attached in a secondary fashion by elements of association of all shapes and dimensions, which we cannot place exclusively either in the sensory or in the motor field, and which consequently will be found in the course of the section.

4. Apparent dissociation of sensation and motion.—The dissociation of sensation and movement is effected in an apparently very definite manner in the two following circumstances: (1) external stimuli applied to our sensory nerves provoke in us conscious *sensations* which are not followed by movement, by muscular effort; (2) movements are produced in our muscles by internal *voluntary* stimulation of the motor system apart from any excitation from without by the path of the senses.

This double observation which every one can make on his own person, seems at first sight to correspond as exactly as possible to the anatomical scheme which divides the nervous system into two sub-systems, one devoted to the exclusive localization of sensation, the other to that not less exclusive of motion.

But this exclusive localizing conception, and the absolute dissociation which it implies between sensibility and motricity, is in reality only based on outside show; it does not survive a somewhat searching analysis. Indeed, as regards sensibility, it is easy to verify the fact that all sensation, such as that resulting from a rather lively external impression, is followed by a *tendency to movement*, if not by actual movement itself. This is a proof that the nervous system is affected in a cyclic manner in its superior portion; the impulse overflows the cortex, and becomes partially involved in the motor paths, since the muscles themselves reveal a trace of it.

So far as concerns the so-called voluntary stimulation of our movements, we have also no reason to believe that this excitation has its immediate starting-point in the motor system, to the exclusion of the so-called sensory elements of the brain. Will implies memory, that is to say, the awakening, the recalling to existence, of one or many *anterior sensations*.

Contrary to strong sensation, which is often only followed by a suggestion of, or by a tendency to movement without any muscular effort properly so called, it is a weak sensation coming on without external stimulation, but followed by effective movements more or less energetic and complicated. It thus implies a cerebral process of a cyclic form, although in certain respects differing from the preceding one.

Inequality of the cycles.—The two cycles, in the examples thus arbitrarily chosen for the requirements of analysis, are unusual in that they have, in the sensory and motor field, prolongations which are not equal, but inversely unequal. They have a common cerebral sensori-motor portion; to this portion, which is of a strictly cyclic form, we see added, as regards the first, sensory peripheral paths from their origin, and as concerns the second, motor paths up to their termination; the motor peripheral paths being, as it were, abstracted from the first, and the peripheral sensory paths from the second. In the first

an actual sensation creates a potential motricity ; in the second, it is an actual motricity, which has for its origin potential stimuli deposited in the brain by anterior sensations. The link, in time, between sensation and movement operates precisely through the permanent cyclic system which we call cerebral.

Extension in surface and depth.—The extension in surface and in depth of the cerebral cycles is, as may be supposed, infinitely variable, according to the nature, the importance, and the complication of the nervous acts considered in an isolated manner. There are some which probably do not pass beyond its thickness and remain confined in restricted areas. There are others which mutually connect its different convolutions, whether neighbouring or distant, at the same time that they connect them with the corpus striatum, the optic thalamus, the cerebellum and the spinal cord in co-ordinated actions.

In principle, it is maintained that the most highly differentiated nervous functions are those which demand the most extended associations, and occupy the largest areas in the brain. For all concerning the surface associations this cannot be doubted, and the constitution of the area for language will furnish an example of it ; but for the deep associations it is better to speak much more reservedly ; one thing, however, is certain, viz. : that intelligence is compatible with curtailments or extensive injuries of the spinal cord, the cerebellum and the cerebral ganglia.

The associations which are affected in the brain and its cortex arise, some between the symmetrical and others between the unsymmetrical portions. The first duplicate in some way (and in a symmetrical manner) the execution of the functional nervous act which is represented in these parts ; at the same time adding nothing to its complication or to its value. It is, on the contrary, the second which give it (as may be gathered) its functional differentiation. The area for speech is also a proof of this. The differentiation presented by it is carried to such a degree, that this centre is confined to one of the two hemispheres, to the exclusion of the other ; this latter, therefore, is unable to participate in the execution of vocal signs, nor, consequently, can it supply the place of the differentiated centre, should this be destroyed.

5. **Multiple connexions.**—The cortical area, corresponding to these limits, is then, by definition, the site of the connexions between the ascending and the descending paths of the tactile system ; but this association, primitive and habitual though it be, is not the only one which can be effected here. By means of the fibres of association which connect it, through the brain, with the other sensorial cortical areas, it can effect sensori-motor combinations other than that which serves as a basis for the present description. It has the power of placing its motor paths at the disposition of another sense (like sight or hearing), or of borrowing those proper to these senses, to attach them to the tactile sensation in some special act. For, in the same way as there are on the surface of the brain a certain number of sensorial areas (as many as there are distinct senses), there are also a corresponding number of motor areas, or zones, each of these areas being sensori-motor, just as the tactile area is sensitivo-motor.

Only, the muscular forces at the direct disposition of the senses other than that of touch being of such small account (muscles of the

ears and of the eyes) in comparison with the number, the extent, and the power of the muscles attached to the sense of touch, the name of motor centre or cortical motor area is in some degree reserved for that part of the cortex which controls the latter.

Effects of destruction.—Whatever may be the realizable connexions, the destruction of the central convolutions severs at their origin in the cortex the cortico-bulbar and the cortico-medullary conducting paths which govern the voluntary muscles of the skeleton ; hence arises the special kind of paralysis by which they are attacked. The same lesion severs at their termination the bulbo-cortical conductors, which convey the impressions received in the skin ; hence arises the anæsthesia which is simultaneously the consequence of it.

6. **Isolation.**—The sensitivo-motor tactile area in this way presents connexions either with the grey axis or with the other sensorial areas ; it is capable of exchanging impulses either with the first or with the second, by fibres which are both efferent and afferent. Experiments have been performed for the purpose of ascertaining how much subsists and what disappears of its activity when these connexions are interrupted either as regards depth or surface. François-Franck, Pitres, Marique and others have cut both the *radiating* fibres of projection which go to the grey axis (by a deep section perpendicular to their direction) and the *tangential* fibres of association (by a circular incision effected around the tactile so-called motor-area).

There is one point on which these authors are entirely agreed ; that is concerning the results of stimulation of the tactile area effected in both cases immediately after these sections. *Section of the tangential fibres alone does not prevent, but that of radiating fibres causes the disappearance of the motor effects produced by the stimulation of the sensori-motor tactile area.* This is a proof that an impulse when originating in the tactile area follows the course of the radiating fibres, and not a round-about route, when going to the grey axis which transmits it to the muscles by its motor nerves ; in other words, its action on the grey axis is a direct one, and this result is in entire accord with the teachings of anatomy.

There is less unanimity as regards the functional modifications which ensue consecutively to these operations. It is true that for both, section of the fibres of projection paralyses the sensori-motor area, and that of the fibres of association allows of something of its activity being retained ; but while François-Franck and Pitres are especially impressed by the preservation of functions in the isolated area, to which, according to their view, a certain directive action over movement is still attached, Marique, Exner and Paneth, on the contrary, insist on

the deficiency following such an isolation, which deficiency they compare to that observed after the ablation of the sigmoid gyrus, though at the same time recognizing that it is less marked.

The points of view taken by these authors are different, but the results are not contradictory. *The isolation of the tactile area from the rest of the cortex allows the persistence of a system* (the tactile system properly so called) *which may still, once isolated, act in an autonomous manner, its functions being necessarily imperfectly performed.*

For, as Exner has remarked, if the sources of motor stimulation are situated partly in the organs of touch, they exist to a still greater extent in the other different senses, which exercise a conscious control over movements. Once isolated from all these senses, the tactile system, reduced to its own resources, will every moment reveal its inability to execute, by itself alone, the functions which were previously performed in concert with all the others. It performs its functions, but in an imperfect manner.

Primary and secondary sensations.—Sensibility is at the foundation of movement; but movement, in its turn, reacts on the nervous system under the form of sensation. There are, as Bastian remarks, *primary* sensations which give rise to movement, and *secondary* sensations which are caused by it, and which, lodged in the nervous system, will serve as guides for a fresh performance of a similar movement. The first can only arise from the organs by which we are placed in relation with the *exterior*, that is to say, the organs of the senses, properly so called; the second come to us from our own organs. In fact, not only the skin, but also the muscles, the tendons, the ligaments, and the surfaces of the articulations are provided with sensory nerves, which gather together and convey towards the brain the *internal* impulses due to movement itself. From this result post-motor sensations, which have been called *cœnæsthetic.* Like those arising from all the other senses, these impressions are stored up in the brain in the state of images or memories. They will be revived more and more easily under the influence of the same causes, that is to say, the same movements, by which they were called into being. Their connexions with these movements will facilitate them, and will allow in the long run of the rapid and precise performance of the most complicated actions. Thanks to the generally cyclic arrangement of the nervous system, the stimuli originally received by it find in it numerous echoes, whose duration is prolonged there in a manner which would not be suspected at first sight: at the same time, they confer a genuine organization on the stimuli, using the word in the dynamic sense which is essential in the case of the living being.

7. Exteriorization of the sensation—The sensations arising from impressions made on the skin, sensations which physiological analysis shows us to be dependent on the integrity of a determinate region of the cerebral cortex, are said to be *exteriorized*, that is to say, brought back to their original cause which has acted on the surface of the integument.

The exteriorization of sensation is a fact common to all the senses. It is evident of itself, and allows of no really satisfactory rational explanation.

Illusions of those who have been subject to amputation, errors of exteriorization.—Those who have had a limb amputated have often a persistent sensation

of the missing member (A. Paré), this sensation being localized by preference in the extremity (fingers) of the lost segment, which seems to be smaller and approximating to the cicatrix. The sensation of temperature in the imaginary limb varies with the real temperature of the cicatrix. Electricity applied to the stump exaggerates these sensations and renders them painful (Weir-Mitchell) ; a prick on the cicatrix is localized in the extremity of the amputated limb. The patient frequently executes imaginary movements with his "phantom limb," and the illusion may be so strong, that serious falls may sometimes result from it. These illusions which, however, gradually diminish, may sometimes last for years.

These sensations, the first of contact (tactile), the second of movement (cinæsthetic), have all, as a starting point, the irritation of the nerves in the cicatrix of the stump, which irritation is *inaccurately exteriorized* by the consciousness. The proof of this is that, if the cicatrix be cocainised, these sensations will disappear (after a short period of exacerbation at the instant the prick is made), to reappear after the elimination of the drug (Pitres).

8. **Localization.**—Not only are tactile sensations exteriorized, that is to say, referred by the consciousness to a cause external to the body acting on its surface, but we can, the eyes being shut, locate them exactly at the point on this surface where the cause acts ; we can distinguish between impressions made on one or other limb, one or other

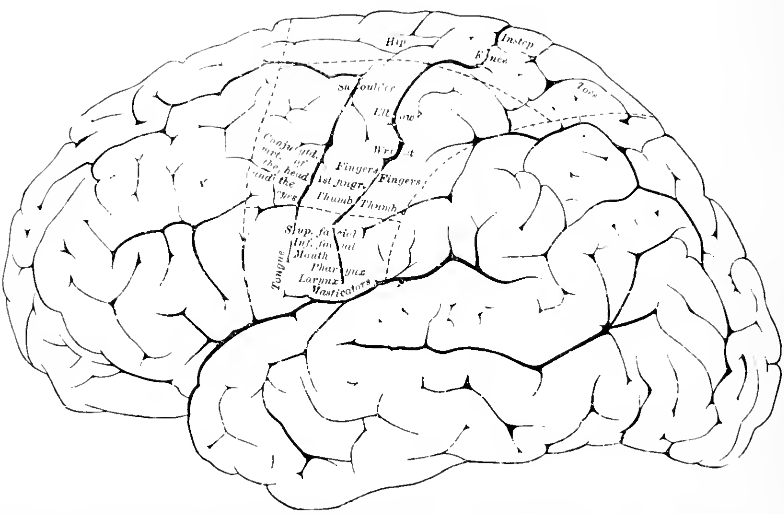


Fig. 218.—The cortical motor area in man as determined by the researches of English and American surgeons, Keen, Mills, Nancrède, Horsley, etc. (copied from Dejerine).

finger, or segment of these parts. This distinction has its origin in the fact that the stimulation affects, in these various localities, different nervous elements. These impressions arrive at the cerebral cortex in different areas, which areas reproduce to a certain extent the topography of the skin. Doubtless the projection from the skin to the cortex is not direct ; the initial stimulation is made on a network ; in the spinal cord the impulse traverses a network once again ; the cortex

itself is a network (not vague and indefinite as was formerly thought, but still a network). In spite of all these complications, it is undeniable that the impulses received in different areas undergo a localization which is prolonged in the nervous system and affects the consciousness in various ways. The proof of this localization is easily found, but its exact formula has still to be discovered. It allows of gradations of whose nature we are ignorant. To deny it is to go against evidence, to push it to an extreme is to destroy the unity of the *ego*. It is marked by contrasts between things fundamentally the same. It has for a support such or such a strongly united system, which on this account has not, however, abandoned all connexion with other systems. A prick on the finger produces a sensation localized to the finger; but, however strong this sensation may be, it does not prevent the individual having consciousness of the rest of his being, and this is why the finger is distinguished and the cause of the sensation localized in it.

C. TACTILE AREA FROM A MOTOR POINT OF VIEW

The tactile sensory area of the cerebral cortex receives impulses coming to it from the skin, which is the initial organ of touch: it itself

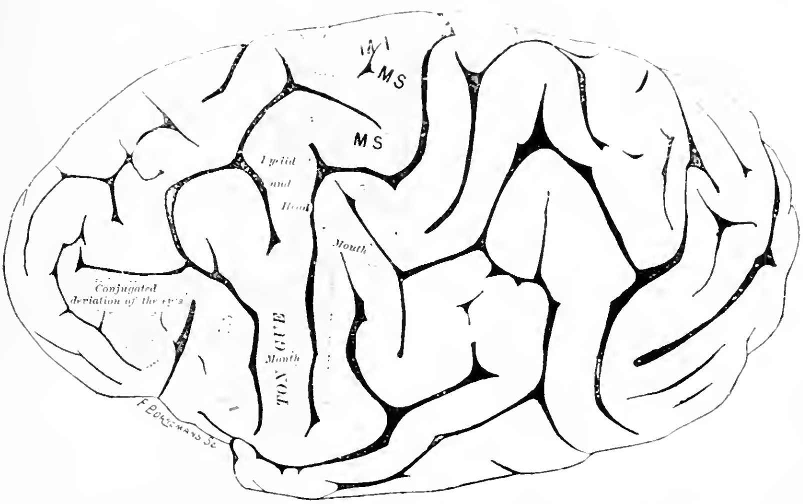


FIG. 219.—Cortical motor centres of the ourang-outang (*Simia satyrus*) (after Beevor and Horsley. *Philos. Trans.*, 1890).

Determination of the cortical areas corresponding to the principal organs of movement. MI, inferior limb: MS, MS, superior limb; tongue, mouth, eyelid and head; special area for the associated movements of the two eyes.

distributes them to the muscles which perform those varied and contingent movements brought into being by our external relations. This area is, as we have already observed, motor as well as sensory: it is one or the other according to whether it is *receptive* of the impulses

which come to it from without through the grey bulbo-medullary axis, or whether, conversely, it *distributes* these impulses to this same grey axis, which transmits them to the muscles attached to the different parts of the skeleton. It is therefore both a *guardian* and also a *modifier* of these impulses, which have already been profoundly transformed and retouched before reaching it, and of which none will attain the muscles without undergoing fresh transformations and fresh retouchings.

The destruction of this area involves a paralysis of the muscles of the skeleton; its stimulation causes these muscles to become functionally active. The paralysis thus produced is not absolute as in the case of section of the anterior roots, when all motricity becomes impossible; it affects certain modalities of movement, which will be suppressed, while others will persist; all movement preceded by a mental representation of the act to be performed will have disappeared. The stimulus will no longer produce the abortive contraction obtained by acting on the roots, but will arouse a co-ordinated muscular effort appropriate to a particular end. Distinctions of the same kind have been made, from the sensory point of view, between the tactile area and the posterior roots; they are essential.

A. Limitation.—From the point of view of movement even more than from that of sensibility, the tactile area is confined to a limited territory on the surface of the cortex. This area occupies the region called Rolandic, formed by the central convolutions, namely: *the ascending frontal, the ascending parietal, and the paracentral lobule*, which is a prolongation of the last-named on the mesial surface of the cerebral hemisphere; it slightly encroaches on the portions which are nearest to the frontal or parietal convolutions.

Divisions.—In the brain itself, and including its surface, something of the same metameric disposition which has been noticed with regard to the roots of the spinal cord may be observed. Primarily, the Rolandic region is divisible into four large areas which correspond to *the inferior limb*, to the *trunk*, to the *superior limb*, to the *larynx*, and to the *head*. These areas succeed each other in the order just indicated; they are arranged in stages alongside the fissure of Rolando, from its superior to its inferior extremity, extending as far as the vicinity of the fissure of Sylvius.

There is, then, on the surface of the brain a supero-posterior region which corresponds to the abdominal member, a supero-anterior corresponding to the trunk, a median region corresponding to the thoracic limb, and an inferior region answering to the head and to the larynx.

Subdivisions.—Each of these regions is subdivided in the same way

as the segments of the parts with which it is in functional relationship. This division is most marked as regards the limbs and the head, these being made up of organs which are, functionally, more differentiated than the trunk. Quite at the superior limit of the fissure of Rolando, a cortical area exists which is functionally connected with the great toe ; immediately beneath it is another area allied to the foot and the other toes, then to the leg, the thigh, the knee. The median region may be divided into consecutive areas functionally related to the shoulder, the arm, the hand and the fingers ; the thumb, on account of its great importance, has a special area situated in the inferior portion of the ascending parietal.

Between the inferior extremity of the fissure of Rolando and the fissure of Sylvius are located in graduated stages the areas of the face, the tongue, the pharynx and of the upper jaw. That of the larynx is at the inferior extremity of the ascending frontal, in the immediate neighbourhood of the so-called motor-centre of speech situated at the base of the third frontal convolution.

Nape of the neck and trunk.—The determination of the motor areas of the nape of the neck and of the trunk has given rise to many investigations and discussions. From the clinical standpoint there is not much evidence on this matter because hemiplegic patients are kept immobile in the recumbent attitude, and the paralysis of these parts attracts no attention, and, indeed, is not usually sought for. Munck, and later Grosglick and Rothmann, located these motor areas in the marginal convolution (first frontal), consequently in front of the pre-central or pre-Rolandic sulcus which separates it from the ascending frontal. It is also very much on the faith of physiological experiments that a centre for the conjugated deviation of the eyes is maintained by certain authors to exist, this centre being situated below the preceding, in the frontal lobe. These results are based on ablations and, more particularly, on stimulation of these different areas, principally on the brain of the monkey.

B. Stimulation.—Artificial stimulation of the cerebral cortex gives rise to an impulse which, after leaving the latter, is conveyed to the muscles and passes through numerous halting places. The first of these is the cortex itself, and the question arises as to whether it modifies the impulse, or whether the latter only traverses it in order to proceed to the subjacent white matter. This matter is itself excitable ; it contains the fibres of projection which descend from the cortex to the basal, bulbar and medullary centres which are more or less immediately connected with the muscles. And being such, it also presents functional localization recalling more or less nearly those of the cortex itself.

Excitability of the white cerebral matter.—Formerly the white matter of the brain was recognized as being as inexcitable artificially as the cortex itself. Burdon-Sanderson, Carville, Duret and many other observers found that it responded to stimuli, as did the grey matter covering it in the localities where this latter is excitable (motor area), and that it gave rise to reactional manifestations of the same nature. François-Franck and Pitres undertook a comparative study of the motor reactions of the two substances. Here are the results :—

Comparison between the excitability of the grey and the white matter.—*The grey is more excitable than the white matter* which lies immediately beneath the cortex ; with an equal intensity of stimulation the motor reaction is stronger in the first than in the second. The grey matter, even in the case of artificial stimulation, would thus possess a power of organizing the impulses which does not appertain to the white matter.

The grey matter impresses on the impulses traversing it a *sensible delay*, which notably prolongs the latent period intervening between the moment of stimulation and the resulting motor effect. This delay, which is $6\frac{1}{2}$ hundredths of a second for a cortical stimulation, falls to $4\frac{1}{2}$ hundredths of a second for stimulation of the corona radiata. It must be observed that the total delay in both instances is much longer than in the case of stimulation of a motor nerve, the latter being of the same length as the course to be traversed, about four times greater. The reason is that the impulse in this course must, as has already been observed, pass through other relays, which retard it on their own account ; the delay is much greater as regards direct movements than for those which are crossed.

The tetanus resulting from cortical stimulation has a certain tendency to persist after the stimulation has ceased, this tendency being much greater than in the case of tetanus due to stimulation of the corona radiata. If exaggerated, this tendency to persistence of the motor effect will become that form of epilepsy which is provoked by excitation of the cortex and of the cortex alone.

Stimulation of the corona radiata has different motor effects (but only as regards intensity) when approaching the internal capsule. This is obviously due to the greater density of the conducting paths, in proportion as the distance from the cortex is increased, on account of the fan or cone-shaped (base uppermost) form of the motor area in the brain.

Variations of the excitability of the cortex ; its conditions.—Many toxic agents modify the excitability of the cerebral cortex. The anæsthetics must be mentioned first : chloroform, ether (Hitzig), chloral (Richet), morphine (Bubnoff and Heidenhain) have a truly elective action on the cortical layer, whose excitability they abolish, while that of the white sub-cortical tracts still persists. Local refrigeration acts in the same manner as also do cocaine (Carvalho) and bromide of potassium, which exert more general effects ; essence of absinthe paralyses the brain and allows of the persistence of the reflex power of the subjacent centres, to which the convulsions produced by this poison bear witness (François-Franck).

On the contrary, strychnine increases the cortical excitability ; local inflammation of the surface of the brain develops it to its highest point. Anæmia of the brain, according to its phases, first augments and afterwards destroys it.

1. **Delimitation of the motor areas by stimulation.**—Stimulation of the cerebral cortex has been practised on all animals, from the batrachia up to the monkey, and even on man himself. It is this excitation which, when methodically applied, enables us to define an area in the cortex which is related to external visible movements and is situ-

ated in the midst of areas called inexcitable, because their stimulation causes no appreciable external manifestation. This motor or excitable region is divided and subdivided into areas which are sometimes

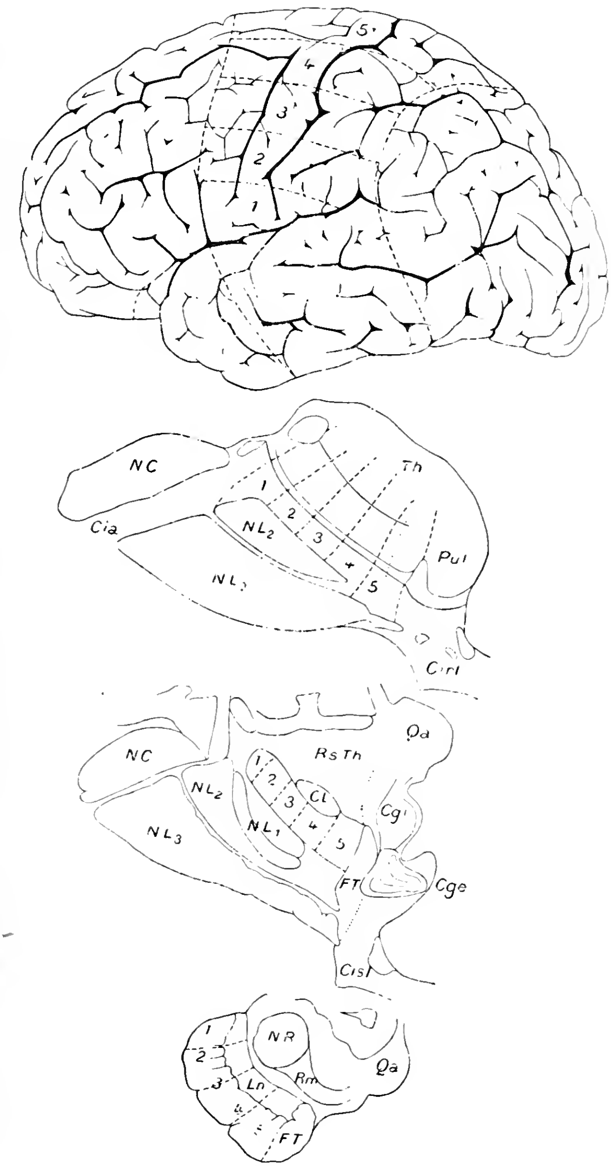


FIG. 220.—Fibres of projection of the cortex, their course, and relative situation in the cortex (upper fig.), in the thalamic and subthalamic regions of the internal capsule (the two middle figs.), in the crus cerebri (lower fig.). Cortex is divided into three sectors (anterior, posterior, middle).

The anterior or frontal sector of the cortex sends its fibres into the anterior segment (*Cia*) of the internal capsule and the anterior portion of the optic thalamus (*Th*). The posterior or occipito-parietal sector sends its fibres into the retrolenticular (*Cirl*) and sublenticular segment (*Cisl*) of the internal capsule; the pulvinar (*Pul*), the external geniculate body (*Cge*), and the anterior corpus quadrigeminum (*Cla*) receive those of the occipital lobe; the posterior portion of the external nucleus of the thalamus and the red nucleus (NR) receive those of the parietal lobe.

The middle sector of the cortex sends its fibres into the knee and the posterior segment of the internal capsule with radiations into the optic thalamus and forms by its fibres alone the crusta (*pied*) of the crus cerebri. This middle sector comprises an inferior temporal or subsylvian segment and a superior fronto-parietal or supra-sylvian segment. The sub-sylvian segment sends its fibres into the sub-lenticular segment (*Cisl*) of the internal capsule with radiations into the internal geniculate body (*Cgi*) and the ventral region of the thalamus; it forms the posterior sixth of the posterior segment of the internal capsule and the external sixth of the crusta of the crus cerebri or column of Türek (FT). The supra-sylvian or superior segment sends its fibres into the knee and the posterior segment of the internal capsule (thalamic region), then into the anterior five-sixths of the sub-thalamic region and into the internal four-fifths of the crusta of the crus cerebri (after Dejerine).

extremely small and which correspond in an isolated manner to distinct muscular regions, as well as to special and adapted movements, recalling those which the animal is seen to execute in the exercise of its voluntary motor functions. These subdivisions of the motor area, which are further superposed to similar subdivisions of the cutaneous sensibility, are numerous in proportion to the elevation in the series of the animal on which the experiment is made.

Another reason why the results obtained through stimulation of the cortex in the monkey are of great value is that the homology of the furrows and convolutions between its brain and that of man is relatively easy to trace, while the type of brain in the carnivora is considerably different from our own. It is stimulation of the cortex in the monkey which has so far yielded the most definite results concerning cerebral motor localization. The relative position of the cortical areas possessing a differentiated motor function has been considered above, and in part according to the information furnished by these stimulations. It only remains to complete this information on several details as follows :—

Cerebral metamerism.—The motor tactile area may be represented as a projection of the muscular system on the cortex of the brain ; nevertheless, the arrangement of the differentiated areas constituting it is not thereby metameric, but is also governed by functional relations. It may be observed that, for a given limb the most powerful articulation, as the thigh and the shoulder, is located in front ; the smaller articulations and those more differentiated as regards movement (great and small toes, thumb and fingers) are located posteriorly.

In the area corresponding to the movements of a given articulation, the stimulus selects those centres which correspond to its principal movements, such as extension or flexion. The first, representing less differentiated movements, are in front, the others behind.

Indeterminate boundaries ; gradual passage from one cortical area to another.—These motor areas, however restricted they may be, have not, between themselves, continuous and fixed limits which would render it impossible to leave one without passing into another and bringing its special effects into action. On the contrary, in each of them there is a *central* point whose stimulation gives the *maximum motor effect*, a point starting from which the effects of the stimulus continue to diminish, to disappear, to be modified and to change direction, when the stimulus begins to penetrate into one of the neighbouring motor areas. The term " centre," often applied to these areas, here retains something of its etymological meaning.

2. **Character of the movements.**—The movements which are caused by stimulation of the cerebral cortex are easily distinguishable from those which may be provoked by stimulation of the other parts of the nervous system ; they display in an eminent degree the character of co-ordinated and adapted movements. This character will be most apparent if it is compared with that of the movements evoked by

stimulation of the motor nerve roots, or of the spinal cord. If, for instance, the motor nerves of a limb are stimulated, movement arises

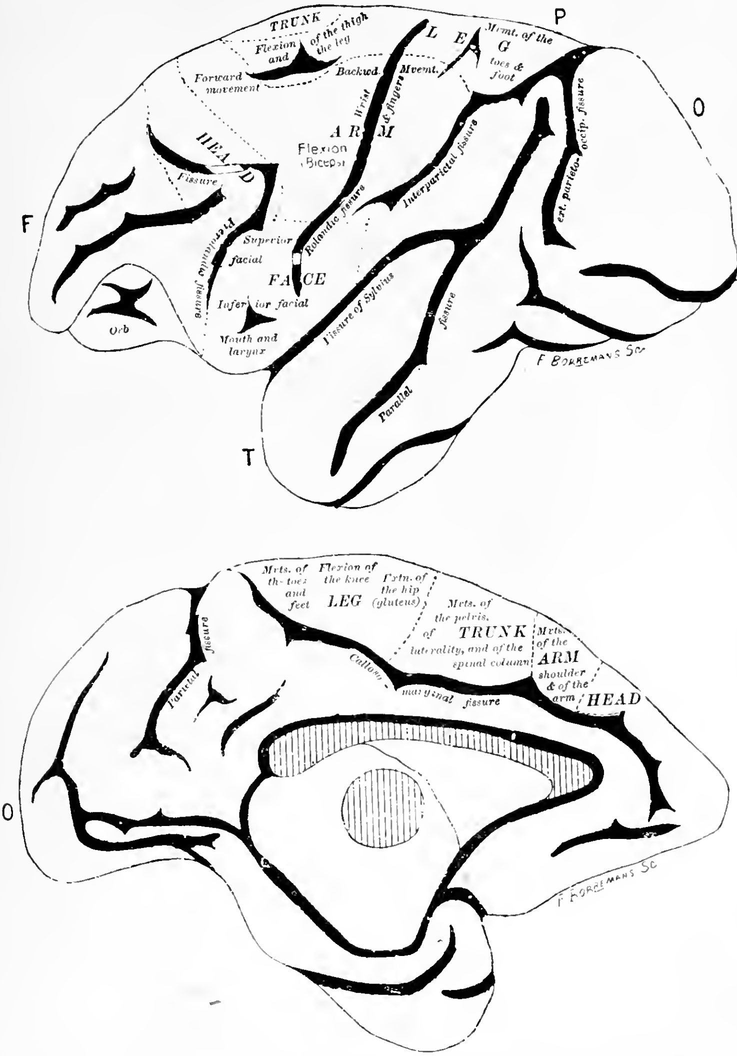


FIG. 221.—The motor centres of the *Macacus sinicus* (after Horsley and Schaffer. *Philos. Trans.*, 1887).

Upper fig., external surface of the brain. Lower fig., mesial surface.
F, frontal lobe ; P, parietal lobe ; O, occipital lobe ; T, temporal lobe.

in the latter suddenly, but the limb is immediately fixed in a rigid position, becoming motionless through the tetanic efforts of antagonistic muscles, its position being given to it by the most powerful of them : when the stimulus ceases, this rigidity also suddenly yields. Stimulation of the motor area of a limb has very different effects : instead of the *impulsive simultaneousness* which follows stimulation

of the spinal cord or of its nerve roots, the muscles of the limb present a *continuous succession of positions*, passing, for example, from flexion to extension or reciprocally, by delineating a definite movement, of the same voluntary nature as those which are controlled by the will.

Primary and secondary movements.—The duration of the stimulation is an important factor in the question ; however short a time it lasts, new motor phenomena will be added to the initial movements. Hence a distinction has been made between *primary* movements (those which are first produced, and are in some way directly related to the point stimulated), and *secondary* movements (being those which only appear after a time, and in segments removed successively from that corresponding to the stimulated spot). From the spot receiving the stimulus the latter seems to propagate itself little by little (by physiological

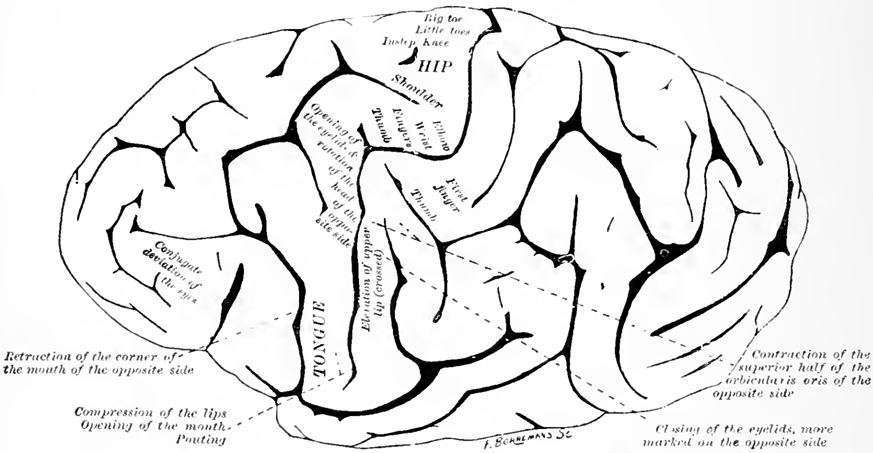


FIG. 222.—Cortical motor centres of the orang-outang (*Simia satyrus*) (after Beevor and Horsley, *Philos. Trans.*, 1890).

Precise location of the movements of the principal segments (hip, shoulder, elbow, wrist, fingers, thumb, forefinger, etc.). Co-ordinate or expressive movements especially of the head (eyes, eyelids, lips, mouth, etc.).

paths) to the neighbouring regions of the cortex, whose functional activities are thus involved by it. This concatenation is not arranged haphazard, but is, on the contrary, harmonious, and somewhat striking motor acts may result from it : extension of the arm and hand to reach an object (ascending frontal at the origin of the first frontal) ; flexion and supination of the forearm with elevation of the hand to the mouth (middle third of the ascending frontal towards the knee of the precentral fissure) ; closing of the fist (middle third of the ascending parietal) ; movements of the posterior limb adapted to seize an object with the foot, or, again, to scratch the chest or the abdomen (superior portion of the frontal and of the ascending parietal) ; opening of the

mouth with protrusion and retraction of the tongue (inferior extremity of the ascending frontal); rhythmical movements of mastication (the same locality a little farther forward); movements of swallowing (same locality, still farther forward).

The inferior portion of the ascending frontal contains, further, the motor area for adduction of the *vocal cords of the larynx*. In the dog this area is situated in the anterior region of the sigmoid gyrus (over the isthmus of the so-called pre-crucial or pre-frontal gyrus); it is thus in the immediate neighbourhood of the centre for the pharynx (that of which the voluntary exercise induces the automatic movement of swallowing), and is also in a sense included in the general area of the muscles of the neck and of the trunk (Munck). The bilateral ablation of the centre of the larynx suppresses the emission of sounds

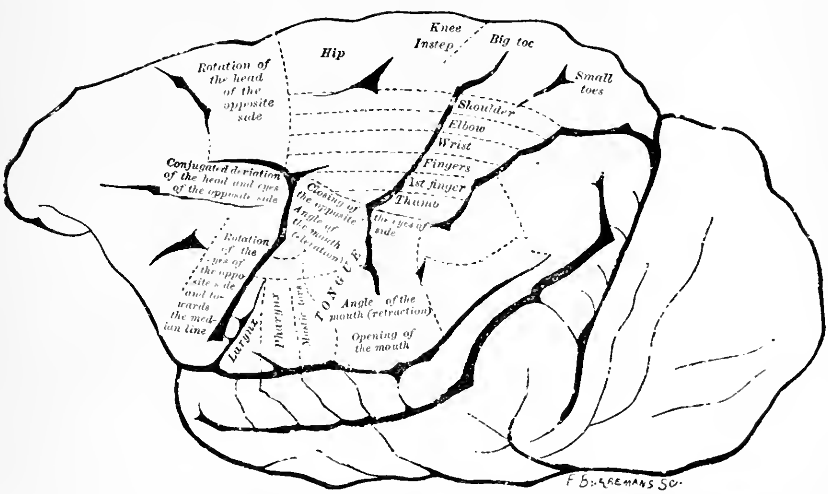


FIG. 223.—Sensori-motor areas of the cerebral cortex of the *Macacus sinicus* (after Beevor and Horsley, *Philos. Trans.*, 1890).

Determination of the cortical areas corresponding to the principal regions of the body or segments of the limbs. Indication of the movements aroused by stimulation of certain of these areas, especially as regards the muscles of the head (eyes, eyelids, mouth, jaw).

(barking), and only allows of the persistence of some feeble cries like those of a new-born animal. It is followed by a secondary degeneration of slight extent, but still recognizable, in the crura cerebri (and also in the peduncle of the mamillary body of the same side); hence there must be fibres of projection which extend from this area to the medulla oblongata.

3. **Motor centre of language.**—In man the posterior portion of the third frontal contiguous to the inferior extremity of the ascending frontal convolution (convolution of Broca) contains an area of extreme importance, that which is named the motor area of speech. It answers

to what is called a centre of association, and, in so far as the expression of the instincts in animals can be equivalent to the language of man, it has also its counterpart in them. In the dog, the motor area of barking is situated, according to Ferrier, at the point of anterior union of the third and fourth external convolution. Stimulation of this region causes, according to this author, a co-ordinated assemblage of movements, giving rise to vocal sounds, attempts at barking, also indeed to a distinct bark ; in this Bechterew agrees. Duret has also obtained similar results. The preceding area has by him been identified with the convolution of Broca, by comparing the distribution of the arteries in man and animals. The removal of this area in a dog suppressed barking for two months, and the animal, like a man who has become aphemic, was forced to undergo a second apprenticeship in order to regain his lost vocal function.

Duret, by lightly compressing this area, has also been able to provoke distinct barking. The stimulation due to the compression is no doubt caused by the temporary anæmia following the effacement of its vessels.

The grey medullary axis and the cerebral cortex.—Stimulation of a portion of the cortex may thus bring into play a co-ordinated system of nerves and of muscles, so as to elicit complex and definite acts. Where is the co-ordination effected ? In what locality of the grey matter ? Obviously the spinal cord

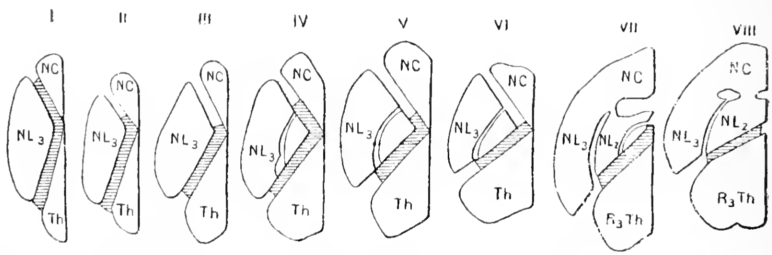


FIG. 224.—The excitable region of the internal capsule of the *Macacus sinicus* (after Beevor and Horsley, *Phil. Trans.*, 1890).

Eight sections of the capsule arranged in stages from above downwards, showing the site and the boundaries of its excitable area. This, at first very extensive, becomes restricted, at first to its anterior portion, is again increased in this direction, once again restricted, and ends by occupying at its inferior portion (sub-thalamic) merely the knee and part of its posterior segment.

takes one share in it and the cerebral cortex another. In movement called primary (movement limited to a segment of a limb and directly dependent on the stimulated spot, therefore restricted and in a sense elementary) it seems as if it were especially the grey matter of the spinal cord which takes part in regulating the motor neurons, and by them the muscles executive of this movement. But when the neighbouring segments participate in the movement, by giving it a more and more complicated form, it must be admitted that the cortex in its turn takes its share in co-ordinating these different systems and elementary

movements into a motor act of a more complex adaptation. Localized in a limited area of the cortex, the stimulus invades the motor field in two principal directions. It extends in depth so as to reach in the first instance the muscles which are in the most direct relationship with the excited area. Further, it extends laterally, bringing into action new regions of the cortex, which, secondarily, send impulses to the muscles with which they are in connexion. The conflicts of these impulses, which are at the same time both motor and inhibitory, determine the direction and the particular form of the movement. But, on the other hand, when localized in a limited area of the corona radiata or of the internal capsule, the stimulus extends only in depth, following the course of the fibres excited, and finds possible associations in the grey subcortical masses in which these fibres end; whence arises the difference in certain cases between the effect of stimulation of the cortex or of the fibres of projection.

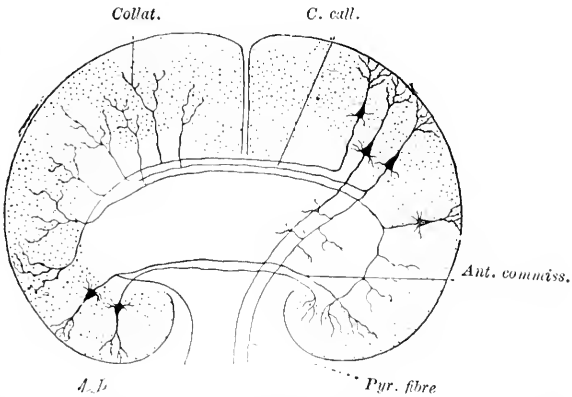


FIG. 225.—The components of the corpus callosum and the anterior commissure.

Diagram of a transverse section of the brain (after Cajal).

Corpus callosum.—The part played by the corpus callosum and, in fact, that played by all the other inter-hemispherical commissures, is far from being understood. In principle it is admitted that the corpus callosum associates the functions of the two hemispheres for the performance of bilateral actions. According to Cajal, the same neuron (a pyramidal cell), which gathers together the impulses in the corresponding hemisphere, distributes these not only by the descending fibres proceeding from it, but also by the collaterals which, arising from the axis cylinder near to the cell, distribute them partially to the opposite hemisphere, by following the route of the corpus callosum; whence the solidarity which is established between the motor elements of the two sides by this transmission of the impulse from one to the other.

Mott, by stimulating the corpus callosum, has obtained bilateral movements of the head, the eyes, the fingers, the shoulder, the trunk, the leg, and the pelvis, but not of the face. If, after the removal of one hemisphere or of the motor area, the longitudinal section of the corpus callosum is stimulated, the movements are unilateral.

Muratoff has observed that section of the corpus callosum was followed by paralytic symptoms similar to those arising from destruction of the motor area. But other observers (Koranyi, Lo Monaco) have denied the occurrence of these effects. It may be understood that, strictly speaking, section of this commissure is not attended with any very apparent paralysis, while stimulation causes positive effects revealed by movements. The same may be said with regard to experiments carried out on the motor area itself.

Co-ordinated sensori-motor systems.—The co-ordinated action of muscular movement is therefore of two degrees. In the first degree

this co-ordination acts in the inferior systems, of which the spinal cord is the keystone ; above this, in a second degree, it operates in the superior systems, of which the cerebral cortex, in its turn, forms the most differentiated portion. A very interesting experiment of Tomasini enables us to obtain a glimpse of the mechanism of this co-ordination.

Experiment.—Before stimulating the motor area of a limb, the posterior roots of this limb are uncovered and cut. Thus the effects of the excitability of the cortex are profoundly modified. The excitability seems changed : it undergoes a first phase of exaltation, then a second one of depression ; but, what is most important, *the movements which were co-ordinated become inco-ordinated.*

At first sight it seems as if the posterior roots have nothing to do with the apparently purely motor phenomenon resulting from stimulation of the cortex. But, in reality, they partly contribute to give to it its essential character. In fact, it is not sufficient that the grey medullary matter remains in its place for the co-ordination to be effected ; it is also necessary that it should have preserved the connexions by means of which it obtains information concerning the movement which it itself produces. The impulse, after its descent from the brain, falls into a cyclic system, in which it circulates in the true sense of the word. This circulation, once interrupted, there is no longer any association between sensibility and movement, and therefore no more possible co-ordination. It is necessary, in fact, for the impulse to reascend to the spinal cord, and even to the brain, from the contracted muscles ; by cutting the sensory roots, the ascending paths are interrupted, and the cyclic spino-muscular and also the cortico-muscular system are broken, whence arises the ataxy of movement observed by all those who have performed this section of the posterior roots in animals which have afterwards been left to themselves.

4. **Direct and crossed action.**—It has long been known that a lesion attacking one of the two cerebral hemispheres is revealed by a paralysis of the muscles of the opposite side of the body, and anatomy has pointed out, in addition to the decussation of the bulbar pyramids, that there are other numerous paths in which the conducting fibres cross, and this may explain the occurrence of the hemiplegia. This simple statement also requires important corrections. It was suggested by the observation of hemiplegics, in whom paralysis attacks (on the opposite side to the cerebral lesion) portions of the body which are immediately obvious, such as the face and the limbs. The features are twisted, the loss of power in the limbs may be complete (the arm being a more differentiated organ is generally more paralysed than the leg).

Paralysis does not, however, respect the side which is supposed to be immune, because this side is obviously weakened, and may even be the seat of paresis ; but the difference of power between the two sides is so great that this weakening is often unnoticed.

Thus *the hemisphere of one side in reality governs the muscles of both sides, but generally very unequally, and much more those of the opposite side :* its action is what is called *bilateral.* It is quite the exception for this action to be distinctly *unilateral.* But this bilateral quality allows of gradations, and at the same time of variety in form. There are muscles as regards which the action of a hemisphere is distinctly bilateral, that is to say, equal on both sides of the body, as, for example, the muscles of the nape of the neck and of the trunk, and, above all, of the vocal cords.

Movements of the eyes.—The action of a single hemisphere on the movements of the eyes is bilateral, in the sense that it is exercised simultaneously on the muscles belonging the one to the eye of the one side, and the other to that of the other side ; but, the parallelism of the visual axis necessary for distinct vision being granted, the co-operating muscles which are controlled by one hemisphere are the external rectus of the opposed side and the internal rectus of the same side ; that is to say, they are unsymmetrical muscles.

But there are also contractions of the symmetrical muscles of the eyes which govern their movements of *convergence*, which is another very important function of these muscles in the association of the two eyes for binocular vision.

Movements of the tongue.—The tongue, which is an apparently median and single organ, presents movements responding to various functions and which, to a certain degree, are analogous to those of the eyes. Some of them are the result of muscular symmetrical actions, such as the protrusion of the tongue or its retraction within the mouth, and are provoked by the excitation of a single hemisphere. These are those which are called bilateral, that is to say, which are bilaterally represented in each hemisphere. There are others, the result of muscular actions which are indeed bilateral, but no longer symmetrical ; such, for instance, is the twisting of the tongue to the right, which is produced by a combined action of the protrusor muscle (genio-hyoid) on the right side, and of the retractor muscle (lingual) on the left, which is obtained by the stimulation of a single hemisphere in a slightly different point from that which produces the preceding movement. In this lateral movement, which recalls the conjugated deviation of the eyes, the retractor muscle is the equivalent of the external rectus of one side and the propulsor of the internal rectus of the opposite side.

In order to dissociate experimentally these two opposite actions, which terminate in a lateral movement, it is necessary to separate the two halves of the tongue by a median longitudinal section (Horsley

and Beevor); it will be seen that, at the moment of stimulation, one of the halves will protrude and the other will be retracted.

In hemiplegic patients the tongue deviates to the side of the injured hemisphere. This deviation, as is well known, is not entirely due to paralysis of the retractor muscle of one side, but also to that of the protrusor muscle of the other side.

The motor cortical area of the tongue contains a certain number of points whose isolated stimulation produces these different movements. At the superior part of this area the movement produced is that of protrusion with lateral deviation; at the middle part a movement of torsion of the tongue, the lingual being directed to the cheek of the corresponding side; at the inferior part, a movement of retraction. These centres are arranged in graduated stages along the fissure of Rolando, from its knee (in the monkey) as far as its inferior extremity.

The mouth and the lips also present various movements of the same kind, often associated with those of the tongue.

Mastication.—Stimulation of a region of the cortex situated at the inferior part of the ascending frontal causes regular and *rhythmical* movements of mastication (alternate lowering and raising of the lower jaw with combined movement of the tongue), lasting as long as the stimulation continues, and ceasing with it.

Swallowing.—Stimulation of a neighbouring area (in front of the preceding one) provokes, one might almost say, attracts a movement of swallowing. It is known that this act is voluntary, in the sense that we can bring it about in ourselves with the mouth empty, but once started we cannot stop it in any one of its phases. Stimulation of the cortex seems to correspond to this initial provocation, acting as a sort of unlatching of the automatic mechanism, and this as much for mastication as for swallowing.

Laryngeal movements.—The movements of the larynx also correspond to various functions and thus enter into numerous associations. Certain of these movements, resulting especially in the adduction and tension of the vocal cords, are *vocal*; they are *respiratory* as regards certain others which ensure their abduction, and in both cases are associated in their turn with different movements of the thorax which stimulation of determinate points of the cortex also elicits. In the dog the centre of these respiratory movements is in the inferior third of the pre-crucial gyrus, and that of the vocal movements lies below the preceding (François-Franck, Lepine, Bochefontaine, etc.). Movements of the larynx (its elevation) are also associated with those of swallowing when the area of these movements is stimulated (Semon and Horsley).

Remark.—That which characterizes the degree of differentiation of a movement, from the point of view of its cortical representation, is not, as will be obvious, its complexity (there are very complicated movements which are automatic ; there are very simple ones which are voluntary) ; it is rather its *contingency*, that is to say, its realization independently of that of other movements, with which, however, it may sometimes be associated, according to circumstances. The movements of the *thumb*, compared to those of the fingers and the toes of the foot, are a striking example of this : they have a cortical representation which is obviously advantageous compared with other movements.

Bulbar and pseudo-bulbar paralyses.—When the motor paralysis is complete, and affects the two sides of the body equally, it is possible that the lesion which has produced it is seated in the medulla oblongata or the spinal cord, localities in which the motor paths of the two sides of the body are approximated and condensed, so as to render them liable to be involved by a single destructive lesion (*labio-glosso-laryngeal* paralysis) ; while the brain, owing to its size and to its division into two hemispheres, is usually the seat of lesion on one side only. But it may happen that very localized cerebral lesions, which are at the same time both double and symmetrical, occasionally produce paralyses affecting both sides of the body : these are the pseudo-bulbar paralyses. They may result from various combinations of cerebral lesions, affecting in the two hemispheres conducting fibres of similar function, but which are injured at variable points of their course, either on one or the other side (cortex, corona radiata, corpus striatum, corpus callosum, etc.) (Brissaud). It must be understood that somewhat marked differences separate bulbar paralysis proper and that known as pseudo-bulbar, both as regards their clinical course and also as concerns symptomatology. The most essential distinction between them is that the first abolishes the reflex movements necessary for the performance of the primordial functions, from which arises its special gravity ; and the second abolishes the voluntary movements.

Epileptiform attacks.—After the stimulation has been several times renewed, the cortex, like all cyclic systems, especially when of a complex nature, retains something of the stimulus after each renewal : and its highly augmented irritability is soon manifested. The stimulation may then cause the appearance of veritable epileptic crises, resembling attacks of *haut mal*.

All animals are not equally liable to manifest this phenomenon. The dog, the cat (François-Franck), and the monkey (Ferrier) are the most suitable. The rabbit, the horse, the ass, the sheep, the goat do not display an epileptic reaction (Albertoni) : the guinea pig, which yields it so easily under the influence of peripheral stimulations, is not liable to any crisis as the result of the direct stimulation of the brain.

The most efficacious excitant is the alternating induced electric current. Mechanical stimulation is but little adapted for provoking the activity of the brain. It is nevertheless efficacious in certain conditions (Luciani), which are indeed those facilitating the development of the epileptiform attacks.

The most favourable condition is that of an *inflammatory* state of the cerebral surface under stimulation.

Characters.—The epileptiform attack is distinguished from the ordinary tetanic attack by the following characteristics : (1) it survives the stimulation after the latter has ceased ; sometimes, indeed, it increases in intensity after the cessation of the stimulus, as if the latter had brought certain arresting influences into play which at first moderated its motor effect ; (2) it has a tendency to be propagated to the muscular groups near to those directly dependent on the stimulated area, and even to spread to the whole of the muscular system of the animal. This propagation ensues gradually according to certain

laws which, however, are not always respected, and from above downwards or below upwards, according to the point of departure. It no doubt acts through the cortical and cerebral paths themselves, rather than through some convulsive

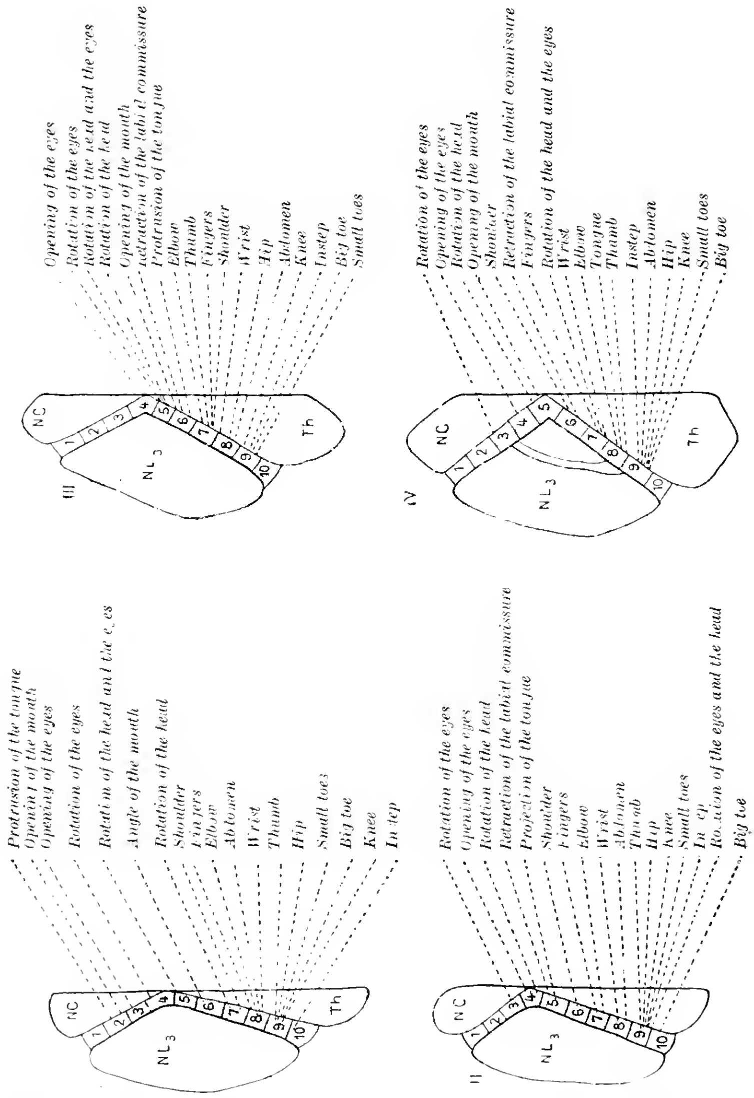


FIG. 226.—Motor capsular localizations in the *Macacus sinicus* (after Beevor and Horsley, *Philos. Trans.*, 1890).

Successive sections of the internal capsule from above downwards.

centre, as has been sometimes supposed. We may add that the epileptic attack arises exclusively from the stimulation of the cortex, and in no sense from that of the white matter whenever the first has been carefully removed (François-Franck).

This character may be likened to that rendered evident by clinical observa-

tion in idiopathic epilepsy, in which the attack is usually preceded by an *aura* seated in some locality of the body, which serves as a point of departure for the convulsions. In man *partial* epilepsies, *hemiplegic* epilepsies and *generalized* epilepsies may be observed.

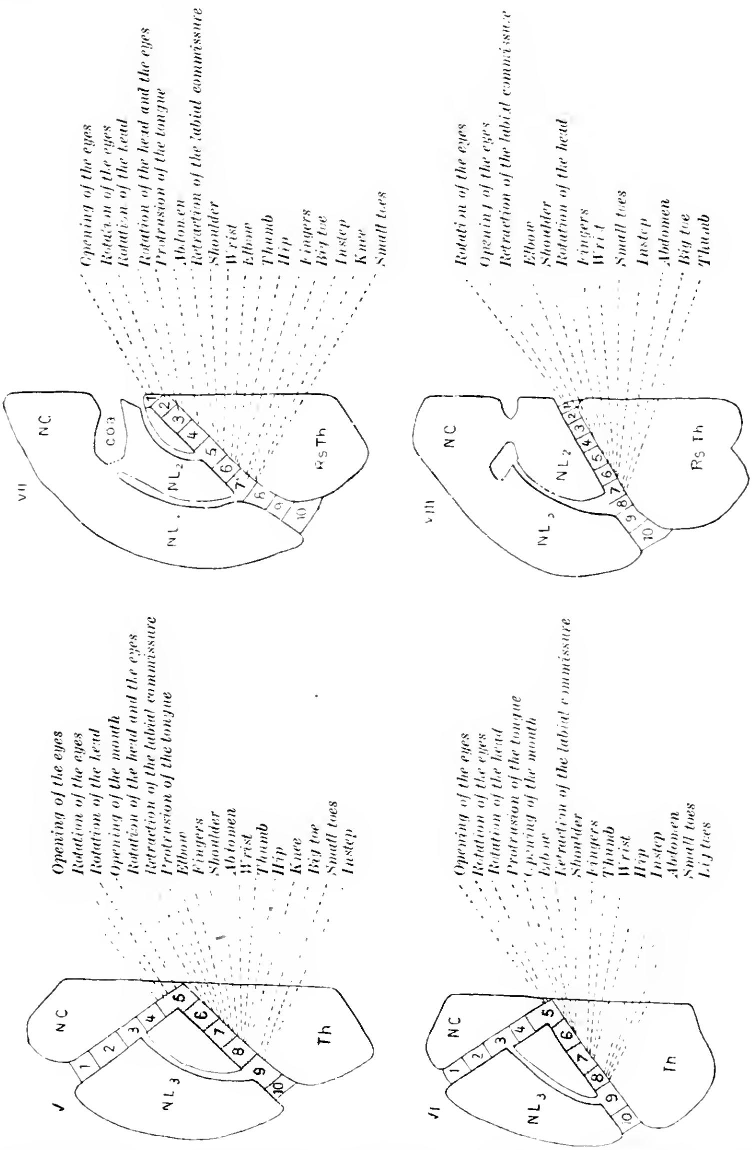


FIG. 226 (*continued*).—Motor capsular localizations in the *Macacus sinicus* (after Beevor and Horsley, *Philos. Trans.*, 1890).

Successive sections of the internal capsule from above downwards.

The comatose condition which follows the attack in man may also be observed in animals. And also, as in man, the attack may, after a time, be renewed without direct, or at least apparent, provocation.

When animals are kept alive after certain superficial injuries of the cortex, attacks of this nature, arising quite spontaneously, may sometimes be observed (Hitzig).

Progress and phases of the attack.—The attack thus provoked displays the two classic phases: the one of *tonic* contraction maintained with slight reinforcements; the other of *clonic* contraction presents dissociated convulsions, which decrease and occur at longer intervals. Sometimes the first of these phases is wanting, and varieties may be noticed as regards the course of the attack. A return to repose is the rule; but according to the intensity of the stimulation, its more or less frequent repetition, the susceptibility of the animal, and the state of the cortex itself, the number of consecutive attacks may be increased; they may become *subintrant*, and death may supervene during the *fit*. Stimulation of the cortex in animals which are kept alive seems to create in them an epileptic tendency.

When once the attack has commenced, if the hemispheres be separated from the sub-cortical centres of the cord the effects are the same. Hence it results that the cortex creates and propagates the initial stimulation into its substance, but that the associations which bring it about are external to it. This fact resembles many others of the same kind tending to the same conclusion.

Internal epilepsy.—The epileptiform reaction thus initiated reverberates on the functions of organic life: there is an *internal epilepsy* which may be dissociated from the other type of the malady, by suppressing the motor effects of the life of relation with curare. Thus dissociated, the internal manifestation is a characteristic one (François-Franck).

Respiration.—Cerebral stimulation usually has different effects on respiration, and manifests, according to circumstances, two tendencies: one to inspiration, the other to expiration, but with concordance of the glottic or other phenomena which assure the performance either of the first or the second of these actions. Stimulation followed by an epileptic attack has, on the contrary, discordant effects, which are rendered evident by the closing of the glottis, the energetic contraction of the muscles of the thorax and of the diaphragm, the augmentation of the intrathoracic pressure, and the imminence of *asphyxia* (mechanism of prolonged effort). This arrest of breathing is interrupted by respirations during the clonic phase. The two phases are not necessarily or regularly concordant with similar phases as regards the muscles of the skeleton. In partial attacks an expiratory condition, without complete closing of the glottis, is most usually observed.

Circulation.—During a severe attack the tonic phase is manifested by a slowing of the heart's action, and the clonic phase by an acceleration of its movements; the reaction being prolonged, however, in a noteworthy manner after the end of the stimulation. During the whole of the attack, the vessels undergo an energetic contraction. This state of the vessels, combined with the preceding changes and with opposite phases of the activity of the heart, often causes the pressure to be augmented, but it may undergo converse variations, in spite of the generally contracted state of the circulatory system.

Pupil of the eye.—The artificially excited epileptic attack in animals is attended by two symptoms which are very characteristic of the attack as observed in man: the first of these is the alteration in the diameter of the pupil which, in epilepsy, is invariably in the direction of *dilatation*.

Salivary secretion.—The second symptom is the secretion of saliva, which occurs at the beginning of the clonic phase of the attack (François-Franck).

Bladder.—There is at the same time contraction of the muscles of the bladder, and sometimes expulsion of urine.

The epilepsy known as Jacksonian.—Limited foci of hæmorrhage and of

softening of the brain often induce reactions of an inflammatory nature in the cerebral cortex, which, by local stimulation of the cortex, give rise to partial attacks of epilepsy (Huglings Jackson). These attacks, according to the nature of their situation, may be rendered evident by convulsions of the face, conjugated deviation of the eyes, etc. The deviations thus produced in the position of the limbs or of the areas affected are naturally the opposite of those which resulted in the first instance from their paralysis. Thus a lesion of the left hemisphere which involves by paralysis a deviation of the eyes to the left would, if this lesion induces epilepsy, bring about a deviation of the eyes in the opposite direction, that is to say, to the right ; according to the mnemotechnical formula adopted in the one case, the patient looks at his lesion ; in the other, at his convulsed limbs.

These partial attacks may also be generalized to a certain extent : in this case the invasion proceeds from the cortical area which controls the muscles convulsed to the neighbouring areas which are progressively affected.

Epilepsy caused by absinthe.—Essence of absinthe, when injected in the blood of animals, gives rise to epileptic attacks in them (Magnan). The convulsions are then of medullary origin, as in this case the poison suppresses the cerebral activity and excitability, while exaggerating that of the medullary centres (François-Franck).

D. MUSCULAR SENSE.—CINÆSTHESIC IMPRESSIONS

The organs receptive of the stimulus in general sensibility are not altogether confined to the skin, and the sensation of contact of external objects, with their qualities of form or of temperature, is not the only one which characterizes the tactile sense. *The muscles receive impulses from the nervous system which provoke them to movement ; in their turn, by their own movements, they communicate impulses to the nervous system.* Thus is made evident the reciprocal influence of sensation on movement, and of movement on sensation.

We thus see that the tactile system receives impulses, some *external*, by the cutaneous surface, others *internal*, by the muscular apparatus. Not only the muscles, but also their immediate prolongations, the *tendons* and the other passive parts of the motor apparatus, furnish impulses, amongst which distinctions have still to be made. The *bones* possess a sensibility of an obscure nature ; the *ligaments*, the *membranes* of the joints, and all those parts which are more immediately submitted to the movement of the levers of the skeleton, are sensory in the same way as the tendons.

Anatomical data.—The muscles, the tendons, the aponeuroses, that is to say, the organs which make or transmit movement, possess sensory nerves. In the muscles, these nerves are very distinct from those which come into contact with the contractile substance of the primitive bundles at the level of the terminal motor plates. Their different characters are as follows : each muscle receives a small number of branches of this nature, of which each is divided into a very large number of ramifications. These ramifications, after having lost their sheath of Henle, their myelin sheath, are finally reduced to bare axis cylinders, which terminate by free extremities. These extremities remain in the inter-

stitial tissue, rarely in direct contact with the muscular fibres, never in the interior of these fibres.

The tendons for their part possess similar terminations, which, after being reduced to bare axis cylinders, are placed between the tendinous bundles and terminate by free extremities, either enlarged, flattened or varicose. In birds,

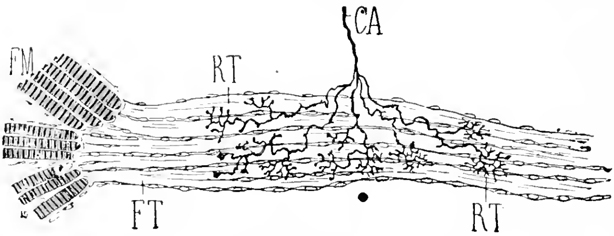


FIG. 227.—Corpuscle of Golgi of the tendo Achillis in man (deprived of its lamellary sheath).

FM, muscular fibres ; FT, tendon fibres ; CA, nerve fibre (axis cylinder bare) ; RT, RT, its terminal ramifications on the surface of the tendon bundles (after M. Duval).

mammals, and especially in man, at the union of the tendon with the muscle, other organs, distinct from the preceding, are found ; these are the *corpuscles* known as those of *Golgi*. They are formed of two or three little tendinous bundles continuous with the muscular bundles ; they are spindle-shaped, and are covered with a laminated sheath lined with endothelium. They are accompanied by from two to four nervous fibres, which, ramified in the form of uncovered fibrillæ, are arranged on the surface of the fusiform bundle (below the sheath of the corpuscle), and, from this fact, present a vague resemblance to the motor terminal plates. They are, in fact, sensory organs ; this has been demonstrated by Cattaneo by means of the method of degenerations. They degenerate after section of the posterior roots, as do sensory nerves ; the motor terminations, on the contrary, degenerate after the section of the anterior roots.

Erroneous terminology.—The expression "muscular sense" has been made use of to designate all the deep sensibilities which supply us with information concerning the execution of movements. The term is, however, incorrect for the two following reasons : (1) the impressions which are furnished by the muscles only constitute a part of the deep post-motor impulses controlling the movement ; a large number come from the articulations, the ligaments, and even from the bones : (2) these impressions are most frequently unconscious, and are on this account distinguished from those of the senses, properly so called, like sight or touch.

Synonyms.—The muscular sense of Ch. Bell has been called by E. H. Weber, the *sense of force*, by Gerdy and by Landry *the perception of muscular activity*, by Duchenne *muscular consciousness*, by Bain *sense of movement*, by Wundt *sense of innervation*, by Hamilton, *locomotive faculty*, by Bastian *kinæsthesic impressions*, and by Bonnier *sense of attitude*. If amongst these designations there are some which are equivalent or synonymous, there are others implying a different conception of the phenomenon which they profess to explain.

Starting point and localization of the muscular sense.—For the larger number of observers the starting point of the impressions, which are at the foundation of the sense of movement or sense of force, is *peripheral*, and located either in the muscles exclusively (Ch. Bell, Gerdy, Landry, Duchenne), or in the totality of the organs participating in movement (Bastian). For Bain and for Wundt, these impressions are, on the contrary, confined to the nervous system itself; they would in the latter be contemporaneous, not indeed with visible movement when about to be realized in the muscles, but with the centrifugal nervous wave which leaves the brain to reach these organs; they would consequently be anterior to muscular movement, thus giving it direction and expression before its performance. The nerves we call motor would be conscious of the movements to which they give rise; and this *without the participation of the sensory nerves;* this, and nothing else, is what sense of movement really means.

This conception appears to us to be quite out of harmony with the principles we have deduced from the examination of the fundamental facts of the physiology of the nervous system. These facts prove most assuredly that the nerves, both those called sensory and those known as motor, are in a strict and reciprocal dependence, to such a degree that it is sometimes difficult to distinguish sensation from motion and motion from sensation; but we are not authorized on this account to maintain that the one can replace the other to the extent of performing the functions of either. The nervous wave which ascends towards the brain is essentially connected with the development of sensibility: that descending from it is, for its part, connected with the execution of movement. No true nervous act is complete in itself except by the association of the two orders of nerves; to maintain that the descending wave can by itself give rise to a sensori-motor act, even one of the simplest, is a physiological absurdity.

Control of the movements by the different senses and the various gradations of the same sense.—Patients who have lost cutaneous, but have retained muscular, sensation, do not suffer any great disturbance as regards their movements; but when there is, at the same time, loss of muscular and osseous sensation the execution of movements becomes very difficult. They may still be performed, however, *under the control of the sense of sight*, but in the dark (or if the eyes are shut) they are very much embarrassed; they are no longer adjusted and proportioned to the end to be attained; they may even become altogether impossible. The patient is unable to realize that he does not perform them, when he has the will to do so; or if, when executing them with the help of the sense of sight, he shuts his eyes, he is incapable of arresting them (Duchenne).

Psychic images of movement.—The question is, however, a very complex one, and analysis, in proportion as it becomes more searching, regards it from more numerous points of view. The performance of muscular movement produces cinæsthesic impressions which, through their appropriate sensory tracts, ascend to the brain and are synthetized into *psychic images* representative of these movements. They are called *motor* images because they become, in their turn, a source of descending impulses, again realizing the movement in its antecedent form. It would be better to call them *sensori-motor* because, though they result in movement, yet they have taken their origin in sensation.

In all these examples the movement is a real one, and we observe it to be, by turns, both the effect and the cause of impressions, of more or less conscious

sensations; but there are cases where the representation of a movement is present in our consciousness, without the muscles bringing it into being. The image of the movement is within ourselves and is a conscious one, while our muscles remain in a state of repose. It may be supposed in this case, as in the preceding, that the nervous action is spread out in a sensori-motor cycle, formed of elements, some of which are ascending and others descending, but which in neither case reach the muscles. This cycle is constructed in the same way as the one connecting the spinal cord to the muscles by sensory and motor nerves, but is situated above it: with the exception that the organs of visible movement are lacking, its action is the same; the ascending impulses are reflected here as descending impulses, and these latter, in their turn, cause ascending impulses to be reproduced which give rise in the consciousness to the representation of a movement having no real existence. This representation cannot be described as an illusion, as we are perfectly conscious of the non-performance of the movement.

Various elements.—Thus in the impressions which have been called cinæsthesic, diverse elements take part; besides cutaneous sensibility, there are at least three more if we distinguish them by the organs which are the starting point of these various impressions: namely, the *muscular sensibility*, the *articular sensibility*, and the *osseous sensibility*.

A. Muscular sensibility.—This is the variety concerning which the largest number of experimental observations has so far been made.

1. **Its proofs.**—*The muscles are obviously sensitive to ordinary stimuli*, such as pinching, pressure, electrization. Their sensibility is particularly obvious in patients who have lost cutaneous sensibility in the regions where the skin covers the muscles. These subjects distinguish distinctly these different stimuli when applied to the muscles through the anæsthetic skin: further, they are conscious of both the active and passive movements of these same muscles, and also of any resistance opposed to their contraction (Duchenne). In animals, if a branch of a nerve which is entirely exhausted in a muscle is laid bare and then pinched, not only is the muscle seen to contract, but evidences of conscious or reflex sensibility are also observed. As a rule, the fibres of the muscular sense are mixed with the motor fibres throughout the length of the mixed nerve trunk (except as regards the roots); but exceptionally muscles may be found to which the motor and sensory fibres are supplied by isolated trunks (Chauveau).

2. **Irritability and muscular consciousness.**—The connexion effected between the motor and the sensory nerves in the muscle, a link which is demonstrated both by anatomy and physiology, has a very important signification. It may be compared with that contracted by the sensory nerves with the motor nerves in the grey matter of the nervous system, and it completes the close concatenation which links together sensation and motion in a twofold manner. The wholly internal bonds uniting

these two phenomena in what we call cellular irritability (of which muscular contractility is an example), appear to us to be, in a sense, exteriorized and rendered visible by the organization of the nervous system.

3. **Sensory nerves of the muscles.**—These deep anæsthesias are met with, in the human species, in morbid conditions, and principally in hysterical patients. They may be induced in animals, more especially in two muscles : the sterno-mastoid and the œsophagus, in the horse. These muscles receive their sensory and motor nerves by distinct paths, which makes it possible to act separately on either and to observe what change will affect the movement when the sensory nerve is cut, and when it is stimulated.

Sterno-mastoid muscle.—The motor nerve of the sterno-mastoid comes to it from a ramification of the external branch of the spinal accessory ; its sensory nerve is furnished by the inferior branch of the second cervical pair. Section of this latter nerve (sensory nerve), when effected on one side, does not alter in any perceptible manner the nature of the movement of the sterno-mastoid muscle when its contraction on one side is compared with that on the other. The movement in question is also a very simple one ; it aids in producing flexion of the head (Chauveau).

Œsophageal muscle.—The œsophagus receives its motor ramifications from the pharyngeal and the external laryngeal nerves : its sensory nerves come to it by a recurrent course from the inferior portion of the vagus, especially from the inferior laryngeal nerve : they may be affected, to the exclusion of the preceding, by cutting the vagi or the recurrent nerves. It is true that these sensory nerves are distributed both to the mucous membrane and to the œsophageal muscle through fibres which are mixed in the recurrent nerves. But it is also known that the sensibility of the œsophageal mucous membrane takes only an insignificant part in the performance of the movement of swallowing, while this movement is continued in the œsophagus with its normal characteristics in the act of deglutition when nothing is swallowed ; and, further, stimulation of the sensory mucous filaments does not induce the reflex movement of swallowing. We may then put the sensibility of the mucous membrane out of court. But section of the vagi or of the inferior laryngeal nerves (sensory nerves) disturbs the peristaltic movement of deglutition to such a degree as to be equivalent to the section of the pharyngeal branches (motor nerves) ; the œsophagus often seems to be paralysed ; it becomes encumbered with food (especially in the inferior part of its cervical region) ; sometimes it suffers from a kind of ataxy which causes it to contract almost

simultaneously and irregularly in the whole of its length. Stimulation of the central end of these centripetal œsophageal nerves gives rise to a simultaneous tetanus of the whole of the œsophageal muscle, similar to that resulting from direct stimulation of its motor nerves, the only difference being that it appears after a somewhat prolonged delay. All these experiments show that the nerves of the muscular sense are essential to the normal performance of the movements of the œsophagus (Chauveau).

4. **Independence of muscular contractility and of the muscular sensibility.**—It will thus be seen that a muscle may be paralysed as regards movements and yet may retain its sensibility, or reciprocally, according to whether certain alterations affect its motor or its sensory nerves. For example, in hysterical subjects, sensibility will be found to have disappeared in certain muscles, and these may at the same time be the seat of contractions which the patient does not feel.

5. **Different modalities of the muscular sensibility.**—Resembling all others, the muscular sensibility displays different modalities, arising in common, but each having a specific aspect. What contributes to give them interest is that disease is capable, in certain cases, of dissociating them. We may distinguish: (1) *sensibility to external stimuli and to compression* which, in healthy subjects, produces a particular sensation, different from that given by pressure of the skin, or of another organ; it may disappear in syphilitic and hysterical patients, and may sometimes be exaggerated in those suffering from lead poisoning; (2) the *sensation of contraction of the muscle,* which is often destroyed in hysterical patients; (3) *muscular fatigue,* which is only an exaggeration of the preceding and which, like it, may disappear.

B. Osseous sensibility.—The bones, like the muscles, are sensitive organs. Their deep situation prevents their sensibility being examined except through the skin, which is itself more sensitive than they are. It has sometimes been possible to test osseous sensibility in cases of cutaneous anæsthesia. Max Egger has shown that the vibrations of a tuning fork, placed on a limb or some region of the body, affect osseous sensibility in a manner almost specific, and not that of the skin. In fact, in the case of cutaneous anæsthesia these vibrations cannot affect the skin. And it is then the corresponding bones which are sensitive to these vibrations, if the anæsthesia is not deep. In the case of deep anæsthesia, they are not perceived when the cutaneous sensibility is intact. The physiologist and the clinician have thus a means of interrogating the osseous sensibility, even through the cutaneous integuments when these latter retain their special sensibility; a tuning fork

yielding 128 vibrations to the second would be the most suitable for this kind of experiment.

C. ARTICULAR SENSIBILITY.—The articulations formed by the heads of the long bones and the membranes, capsules, or ligaments uniting them, are sensitive, inasmuch as these different structures are provided, like the tendons, with organs receptive of impulses and centripetal nerves. The tension of the ligaments and the rubbing of the surfaces in contact produce these stimuli.

Experimental dissociation of the cutaneous and deep sensibilities.—The lower limb of the bird has been made use of to bring about this dissociation experimentally. The absence of muscles in the foot of the bird allows, by cutting the nerves which enter into this extremity, of the complete abolition of sensation in the toes without compromising the motricity of any of the muscles of the leg. The section suppresses, it is true, sensation in the articulations of the foot, but leaves intact that of the muscles. The bipedal position of birds in standing still and walking renders this experiment a very striking one.

Chauveau, in tame pigeons, having cut the four nerves of the leg around the articulation of the tarsus, studied the result of this insensibility.

(a) *In repose.*—During sleep, the subjects perched quite indifferently either on the enervated or the intact foot, and also on both together.

(b) *In walking.*—" When the subject was placed on the ground after the operation, it seemed to experience some hesitation in using the enervated foot as a support while walking. But this hesitation did not last long. It was shown, at the moment of starting, by the repetition of the movement of placing the claws of this enervated foot in contact with the ground. The animal appeared surprised not to feel the contact with the latter. But, once it had begun to walk, the pigeon used this foot as freely as the other."

The precision of the movements and of the attitude in these experiments shows how little cutaneous sensibility is necessary to the co-ordination of efforts in order to ensure their normal performance. Muscular sensibility, obviously retained, must play here a part of the utmost importance.

1. Conceptions furnished by the different sensibilities.—The ideas and the information furnished us by the different sensibilities, both deep and superficial, are numerous. Through them we ascertain if our limbs and our body are in a state of *immobility* or of *movement ;* to them we owe the power of distinguishing in ourselves a *static* from a *dynamic* condition, and they are further capable of defining precisely each of these two states.

Notion of the position of the limbs.—In fact, by measuring these impressions, we obtain an idea of the positions of our body and individually of our limbs in the varied position which these are capable of assuming and preserving. This conception is abolished if both cutaneous and deep sensibility become paralysed. This loss of the idea of position is often observed in pathological conditions of the nervous system.

The idea of the position of the limbs probably comes to us from impressions

gathered together in a permanent manner, either by the skin in contact with external objects (ground, clothes, sheets, etc.), or by contact of the limbs between themselves (folding, or tension of the skin, etc.), either by the osseous levers and especially the articulations; or by impressions equally permanent resulting from the mutual tensions or pressures of the surfaces, and which vary according to the relative position of these articulated levers. We have already remarked, with regard to the functions of the sensory roots, that a permanent flow of impulses reascends throughout the length of these conductors, and that this flow is of very varied origin.

2. **Cortical localization of the muscular sense and the cinæsthesic impressions.**—The muscular sense and all the sensibilities which we call deep are, individually, most usually subconscious or even unconscious; but they nevertheless furnish us, by their associations, with conscious conceptions concerning the state of our bodies, however little the attention is directed to it and its different mobile segments. The impressions proceeding from the deep portions of the limbs reach the cerebral cortex, as do also those coming from the skin. They form in the cortex, and even before reaching it, numerous associations. The cortical area receiving them is none other than that which we call the tactile area situated in the central convolutions of the Rolandic region.

Several proofs may be given of this. If, as Tonnini has done, this region in animals be destroyed, disturbances of the muscular sense are invariably observed. If the limb corresponding to the region destroyed be placed in an uncomfortable position, the animal retains this attitude without troubling to alter it, which it would do at once if it had any consciousness of this discomfort, that is to say, if the deep sensibilities (above all muscular) were retained, even though cutaneous sensibility might be lacking. Further, disturbances of the muscular sense are those which persist the longest after these destructions, as a number of authors have observed.

Dana, in view of surgical intervention, having laid bare the middle region of the right ascending frontal convolution, electrically stimulated this region of the cortex: contractions of the left arm and shoulder ensued, and also a sensation of swelling and of heaviness in the corresponding limb. The stimulation produced neither pain nor a feeling of contact, but a sensation which, in our opinion, much more nearly resembles the manifestations of muscular or deep sensibility. It must, further, be recognized that in this observation the succession of motor and sensory effects may be very complicated, and that it would not by itself point out to us the locality of the brain in which are situated the cinæsthesic impressions, arising from the movement, which evidently results from the stimulation of the cortex.

Idea of the movement of the limbs.—By these different sensibilities, and especially by the cinæsthesic impressions, we obtain, on the other

hand, the idea of the movement of our limbs. This movement may be either passive or active.

Passive movement.—Passive movement is a more or less abrupt change of the position of our limbs ; we appreciate it by means of the same sensory elements as this position itself, and we estimate it by the change supervening in the impressions which these elements give rise to.

Active movement.—In active movement we are conscious, not only of the position of our limbs and of the gradual change supervening in this position, but also of something added to this, namely, *a feeling of effort.*

Sense of pressure and sense of force.—If when the hand is extended with its dorsal surface on a resisting plane, we place on its palmar surface gradually increasing weights, we can estimate within certain limits, the absolute and relative value of these weights ; or, to put it otherwise, the degree of pressure (or better), compression, exercised by them. If, with the palm of the free hand, we weigh these weights, we can also appreciate their value ; and this second proceeding will furnish a much more exact estimation. In the first case, our resistance to the pressure of the weights is purely passive and the stimulation we receive from it is localized in the *cutaneous* sensibility ; in the second, certain of our *muscles* intervene actively, to resist the pressure of the weights and to balance it ; the *muscular* sensibility intervenes conjointly with the cutaneous sensibility to give us the appreciation we are in search of.

3. **Feeling of effort.**—Nothing is easier to verify, but nothing more difficult to define, to analyse, and to localize, than this fact of internal observation. Nevertheless, it is quite fundamental ; for it is at the origin of the distinction we draw between ourselves and that which is external to us. *That which, from the beginning of our existence, appears to us as being outside ourselves, that which resists us, or which we are resisting.* By the external forces that we overcome, that we balance, or submit to, we become conscious of our own particular force and we determine the plane of division which distinguishes us from them. Effort symbolizes, by an elementary example, what is commonly understood under the name of *activity*, another term of which we have a clear conception, but which it is quite as difficult to define.

The value of effort, so far as it concerns the fundamental element of the formation of consciousness, arises from the close association and the reciprocal dependence in which movement and sensation are here found in it, a dependence and association which are characteristic of

the living being, and which the cycle of impulses proceeding from the muscle to the nervous system and from the latter to the muscle, realizes in the most direct and visible manner. From it arises the first rough sketch of our personality. When the skin, the eye, the ear, that is to say, the paths of the senses properly so called, are in their turn open to external stimuli, they complete, strengthen, and determine precisely the fundamental ideas provided by the muscular sense, but they find these essential ideas of consciousness already constituted.

Muscular effort, psychic effort.—In the order of sensibility, we draw a distinction between an impression made at the periphery and a sensation which does not develop itself clearly except in the superior portions of the nervous system. In the order of sensibility, we distinguish in the same way between a purely muscular effort which is exerted by our muscles against external objects, and a psychic effort proceeding from the superior portions of the same system in order to arouse muscular action. We will consider these two phenomena, first alone, then as regards their connexions.

Analysis of the phenomenon.—Taken individually, the two phenomena of sensation and muscular effort may at once be pronounced to be cyclic phenomena. Sensation implies a tendency to movement, effected more or less feebly in the muscles which are the most directly in connexion with the surface on which the impression is made (adaptation of the hand to the surface) of the object touched (active touch). The psychic effort, in its turn, implies a sensation immediately consecutive to the movement produced (sensation of muscular activity, of displacement of the osseous levers and their soft parts, resistance of raised weights, etc.). We here find once again the double reciprocal link between sensibility and movement—a link of such a nature that, were it to be completely broken, it may be assumed that neither sensibility, nor effort, nor any nervous functional act, would any longer be possible.

The analysis may be carried still further. If we cut away and destroy the superior systems, sensation and psychic effort, properly so called, disappear, and are replaced by reflex acts which only represent them in an extremely attenuated form. Yet in these reflex acts we find, once more, the same double link, between sensibility and movement. From the fact of the existence of this link certain reflex acts acquire the possibility of subsisting automatically in an indefinite manner when movement has once begun in them (respiration, regulation of the nutritive functions). If we disorganize the interior systems by cutting the peripheral nerves, sensation does not irrevocably disappear, but may be prolonged and reawakened in the condition of remembrance: the cerebral phenomenon, thus unloosed from its connexions with external provocative actions, takes the name of *psychic*; it is certainly connected with the persistence of internal reflex cycles which preserve the impulse and prolong the sensation in a manner which is fundamentally automatic. In an individual whose brain is intact, but whose spinal motor nerves are paralysed, the psychic effort is still possible. Such an individual has a very distinct representation of the movements which he wishes to execute, but which he is prevented from performing by his peripheral paralysis. It must be assumed that, in this case also, the cerebral process is of a psychic form: to the descending impulses which leave the cortex and which are not stopped in their journey before reach-

ing the muscles, succeed others which ascend to it by reflexion of the first on the subjacent centres, and bring into action the nervous mechanism in all that is essential. Reflexion, with recall of precise sensations and definite representations of movements (but without actual impressions as regards the first, or execution as concerns the second), can only be rationally explained by a process of this nature, a process made in the likeness of that which brings actual sensation and voluntary movement into being, but which is confined to the superior portions of the nervous system, and is for this reason purely representative.

4. **Voluntary stimulation.**—When movement follows immediately on an unconscious impression, we call it reflex ; when it follows inevitably a vividly felt impression, we call it psycho-reflex or emotional ; when it has no connexion with a stimulus or an actual sensation, we call it *spontaneous* or *voluntary*.

Movement appears to us to be here independent of sensation, and the dissociation of these two phenomena seems complete. It is so only in appearance however. Voluntary determination arises from ideation, from reflexion, and this in its turn proceeds from sensation. But *the determination* which we call *voluntary* has about it this peculiarity : that, *while keeping its connexion with sensation, it may be adjourned in time in an indefinite manner ;* and as, during this delay, the brain receives new impulses, which it has the power of preserving automatically, and is also capable of associating and reassociating in numerically infinite combinations, the postponement of the movement, as well as its extreme variety, disguises its true origin, which can only be in an external stimulus.

Thus the will does not reveal a spontaneity of impulses, but a very profound transformation of them in their passage through the brain, a transformation in virtue of which they are mutually associated in the whole compass of this organ and may also be connected in time. Hence there results, as regards the individual, a sort of appropriation of the objects surrounding him, which he condenses in himself under the form of representations ; there also results for him a number of motor possibilities in a way almost unlimited and practically a great power over these same objects. The sentiment of motor spontaneity existing in us has its origin in a process of internal analysis which compares these different motor possibilities between themselves, and which, by foretelling their consequences, gives a preference to one of them, after a series of mental experiments which are not followed by action. Without *hesitation*, we should not know the meaning of the will. Reflex action narrowly resembles a physically determined movement ; it acts without hesitation, that is to say, without delay ; voluntary effort is a movement which is at the same time physically

and psychically determined, that is to say, in which the determinism is present in several degrees.

Sensation and movement in the fœtus.—The fœtus, while still *in utero*, exerts movements which are known as *active* and which are regarded as *spontaneous.* When the origin of these movements is taken into account, it will be obvious that they would be more accurately described as *reflex.* In the first instance, the fœtus seems to be protected against every external excitation by the maternal organs; this is certainly true so far as regards merely shock from external objects and the specific excitants of the senses (light, sound, etc.). But the structure which encloses and protects the fœtus (the uterine muscle) is also capable of exciting it by its contractions and by the pressures which result therefrom. It would seem, therefore, to be quite reasonable to maintain, with Féré, that the movements of the fœtus are merely the reaction of its nervous system against uterine contractions; and that, whatever may be the degree of consciousness with which they are accompanied frcm their first appearance up to the moment of birth, their reflex origin cannot be denied.

Reactions of the uterus to excitations proceeding from the different senses.—Like all other visceral movements, the contractions of the uterus (during pregnancy) are not perceived by the mother; as a matter of fact, these excitations frequently occur, and are the result, like those of the vessels, of the intestine, of the bladder, etc., of every somewhat marked excitation of any one of the senses. It is a fact well known to all those who are in the habit of performing experiments, that such excitations react on all these organs, giving rise to contractions, in them, even apart from their functional activity properly so called. The uterus forms no exception to this rule; it is these contractions to which the fœtus is subjected, and which furnish it with the first idea of that which exists external to itself. Hence there are reflex movements of the fœtus consecutive to maternal uterine reflexes. It follows therefore that *the origin of fœtal movement is invariably an external excitation; this excitation must pass through the maternal nervous system before it can attain its own special nervous system*, exactly as its nutritive materials pass through the maternal blood before entering its own. All the specific excitations which affect the maternal senses are thus transformed and brought back to almost uniform mechanical excitations, which act on the fœtus, and through them it receives its first lessons as regards sensation.

CHAPTER II

VISUAL INNERVATION

LIKE touch, with which it has so many points of resemblance and so many connexions, vision is a phenomenon which is at the same time both passive and active. We *see* the objects which present themselves to us; further, we *look* at those which our attention points out to us. The motor and sensory acts succeed each other as it were in cycles, which the intervention of the other senses complicates and enlarges in proportion as it augments the sources of our knowledge.

The sensori-motor system appropriated to the sense of sight comprehends (like all other systems of the same nature): at its origin, differentiated receptive elements, the rods and the cones, adapted for the reception of luminous impulses; at its termination, muscles which turn the eye towards that locality in space to which it is directed in order to seek this stimulus: between the former and the latter are reflex arcs, whose complexity goes on increasing with their length, causing the impulse to penetrate more deeply, from the retina up to the cerebral cortex. It is the constitution of these arcs, infinitely variable according to the case under consideration, which forms the basis of the study of visual innervation. On the surface of the brain an area may be approximately delimited which represents the deepest locality where these impulses are reflected, a kind of surface of projection which they only attain when they are to become conscious (visual area of the cortex distinct from that of the other senses). At the periphery a still more distinctly defined field, that of the two retinæ, represents the surface of reception for luminous impulses; as for the muscles to which the stimulation returns, these in principle may be all the muscles of the body, but as we are concerned with the analysis of the phenomenon, we will specially consider those directing the visual axes, namely: the rotatory muscles of the eye, the head, or even of the body.

From the retina to the brain the impulses traverse, or coast along, certain localities of the grey matter, which may send them back unconsciously to the protective muscles of the eye, or to certain internal

muscles, which also exert protective functions and those of adaptation for this organ as regards the luminous agent.

A. FROM THE RETINA TO THE CEREBRAL CORTEX

The retina, a thin membrane which carpets the deep portion of the eye, presents in its thickness three superposed neurons (more exactly, two neurons and a portion of a third). These are : (1) the *rods* and the *cones* (the last in the yellow spot and the first in the rest of the membrane) ; (2) the *bipolar* cells known as *visual ;* (3) the cells known as *ganglionic.* These last give rise to axons which form the fibres of the optic nerve and ascend towards the cortex.

1. **Morphological signification.**—As regards the whole of the sensori-motor systems into which the nervous system is divided, a unity of plan is admitted as also a sort of equivalency between their component elements. In the series of neurons forming each of these partial systems it may readily be allowed that there exists the same number of elements and principal halting places passed over by the impulse. We may then attempt to group these in numerical order, by comparison of one system with another. In the tactile system the initial neuron is that which, from the skin, proceeds to the grey medullary matter, where the impulse is taken up by a second neuron which reaches the encephalon. In the visual system, the initial neuron is a rod or a cone which transmits the impulse to a bipolar cell ; this, in its turn, passes it on to a ganglionic cell or to the origin of the optic nerve. Thus it is tolerably clear that another element exists, over and above that contained in the preceding system, taken as a type of structure. An effort has been made to re-establish homology by comparing the rod and the cone, no longer to a nervous element, but to a differentiated epithelial cell resembling those which are found at the extremity of the nervous tactile terminations ; in this case the equivalents of the neurons of the posterior roots would be the bipolar cells. If an intravascular injection of methylene blue be made on the living animal, the rods and the cones will undergo no coloration, while the bipolar cells and all the strictly nervous elements of the retina will be coloured by this reagent (Renaut).

Fundamentally, it must be admitted that, in all these systems, we do not know the exact mutual connexions of the nerve elements. We are ignorant whether there may not exist, between the first and second tactile neurons, some short interposed neuron of the same nature as the bipolar cell of the retina. And, further, the unity of plan may not be of so rigid a nature as to imply a number of exactly similar elements in all the analogous systems.

Cells of association.—Besides the neurons which seem thus to be placed in direct succession to each other, cells exist either in the spinal cord or in the retina, which are provided with short prolongations; these are called cells of the neurons of association, because it is supposed that they establish between the nervous conducting paths relations other than those arising from the direct contact of these last-named. A knowledge of the manner in which these associations are carried out would be of the very highest interest to us, but at present this information is wanting. We can but suppose the connexion to be of a very complicated nature. In the layer of the internal granules of the retina are found small and large horizontal cells to which a function of this description has been assigned. Other cells called *spongioblasts* have also been observed whose single expansions are connected with the ganglionic cells of the retina. The retina, while presenting abbreviated structures, which elsewhere attain large dimensions, is, nevertheless, a more convenient locality than are those others for the study of the connexions under discussion. More particularly, it displays the following detail, also observable in other senses, namely: that in their articulation, the neurons do not correspond each to each, but that their field of distribution overlaps portions (it may be unequal portions, according

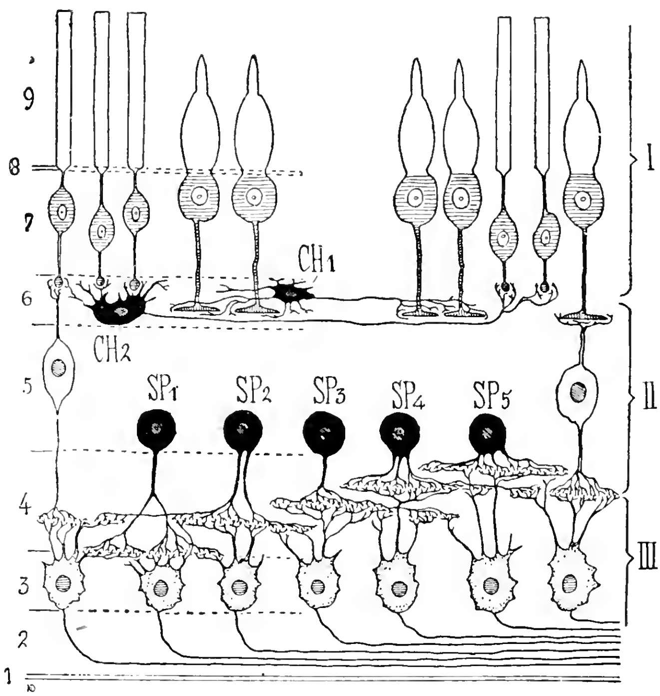


FIG. 228.—The retina (diagram, after M. Duval).

1 to 9, the nine layers of the retina; I, II, III, the three superposed neurons which form its elements placed in succession; I, visual cells; II, bipolar cells; III, ganglionic cells; CH and SP, neurons of association: CH, small horizontal cell; CH_2, large horizontal cell; SP to SP_5, the five orders of spongioblasts.

to circumstances) of the fields of reception of the consecutive neurons.

2. **The retina is a nervous centre.**—However it may be with regard to these details, we must conclude that the *retina*, speaking generally, *is the equivalent of the grey bulbo-medullary matter.* It should be regarded as a portion of this matter separated from the rest, and brought during its development into the vicinity of the periphery. The optic nerve is not the equivalent of a posterior medullary root, but rather of a white tract of the spinal cord, which has become involved in the orbit for the purpose of uniting the grey retinal matter to the encephalic centres (ganglionic and cortical).

Gradation of the grey masses.—The fibres of the optic nerve, after having passed through the chiasma, are found (some after dissociation and others directly) in the *optic tracts*, and these end in three very remarkable localities of the grey matter : *the external geniculate body, the anterior corpus quadrigeminum, the pulvinar of the optic thalamus.* This latter gives its significance to these centres as a whole. The ganglia of the base of the brain, and especially the optic thalamus, are, as is now known, the principal terminations of the conducting paths of sensation, both general, tactile and sensorial.

The optic thalamus is divided into segments, of which each answers to a determinate area of the cerebral cortex (Monakow) ; the pulvinar represents the segment corresponding to the occipital lobe and appertaining to vision.

The pulvinar, the corpus quadrigeminum and the external geniculate body are often described by the name of primary centres of vision. This designation should be rejected, inasmuch as this stage of the grey matter is really the second, the retina being obviously the first.

3. **Optic radiations.**—From the ganglia of the base of the brain the impulse (whether it passes through them or only skirts along them) becomes involved in the fibres which conduct it up to the cortex, to an area thereof occupying the borders of the calcarine fissure. These fibres form the *optic radiations* or those of Gratiolet ; they arise in an intricate mass of fibres (field of Wernicke) confined to the pulvinar, and, skirting more especially the internal surface of the posterior horn of the lateral ventricle, spread themselves out in the cortex on the internal surface of this lobe.

Long paths and interrupted paths.—The same question which has already arisen as regards the other senses once more confronts us here. What is the value and signification of these different stages of the grey matter ? What is the choice here effected between the conducting elements ? And what connexions are here entered into by them with the new elements arising in it ?

In principle, we know that the impulse here finds paths of return, which bring it back to the motor organs endowed with psychical qualities, but with less of these in proportion to the shortness of the reflex arc; that is to say, in proportion as the reflex arc is less involved in the depths. But this is not sufficient. The impulses which are not reflected, but, on the contrary, conveyed towards the cortex, also seem to undergo a transformation therein, whose modalities and precise mechanism escape us.

Anatomy merely demonstrates this: of these halting places of the grey matter, the first represent complete interruptions, all the fibres ending therein to re-arise, following new connexions; the retina and the grey medullary matter are halting places of this kind: the second are only partial interruptions, a part of the fibres distributing their terminal arborizations there, while the rest pass through them without solution of continuity to terminate in some other grey nervous mass. The pulvinar, the corpora quadrigemina, the geniculate bodies, all the basal ganglia, are included in this category. The grey bulbo-medullary axis (with its sensorial equivalents) and the cerebral cortex would thus be the two localities where the grey matter would have its most

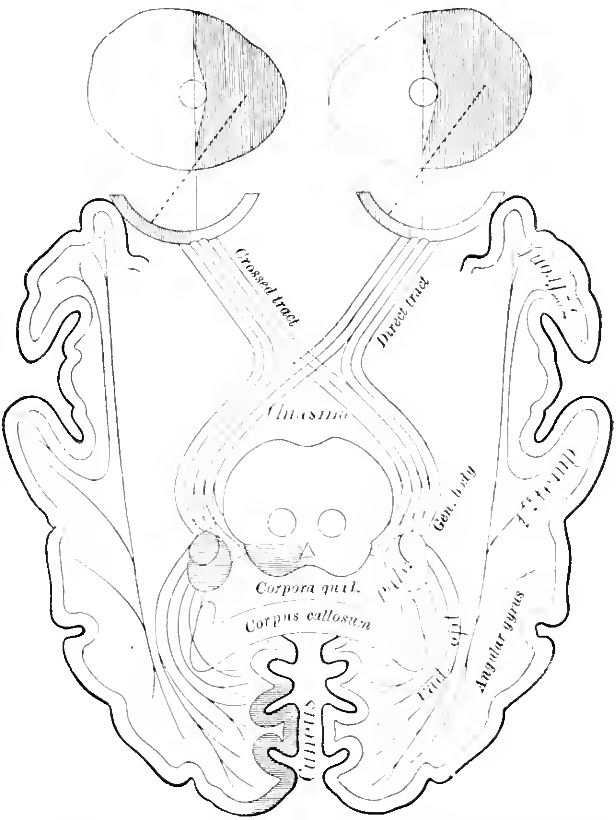


FIG. 229.—The visual system: its sensorial paths (diagram copied from Vialet).

The cuneus, the pulvinar, the corpus quadrigeminum, the external geniculate body and the half retina of the left side are marked by hatching, and also the portion of the visual area of each eye corresponding to them.

Associating tracts unite the occipital lobe and the angular gyrus to the convolutions of the area of speech, and in the latter the first temporal to the third frontal.

marked morphological character. This, however, is only a question of degree, since the boundary line of these areas and their distinction from the white matter are not in the least absolute. However this may be, some maintain the possibility of the existence of fibres (in small numbers) going directly from the retina to the cortex, skirting the intermediate centres ; these are the long or direct paths ; the other conducting fibres are arrested and arranged in series in these different centres, or else associate them amongst themselves ; by comparison with the others, they are *short paths* which, as a whole, may be called *interrupted paths* in opposition to the preceding.

4. **Progressive transformations of the nervous act.**—The problem is no longer, as has for a long time been imagined, to find some sort of a path which would either by itself alone, or by the union of its contiguous segments, project the impulse received at the periphery on to the cerebral cortex, this definitely giving to the nervous act its psychical qualities. Everything, on the contrary, tends to prove that these qualities are only acquired progressively, by successive processes, leaving nothing for the cortex but a completion of the work by utilizing elements which have been previously elaborated. What is the part played by the short and interrupted, or long and direct paths in this preparatory process ? To this question the facts at present at our disposal do not provide us with a satisfactory answer. Are these paths employed separately for distinct functional acts ; and, if so, for which ? Or are they employed simultaneously in the most complicated aggregated acts ? These also are questions to which no answer can be given, but which it is necessary for us to propound.

5. **Dispersion of the impulses in the system.**—The succession of impulses following the nervous paths from the retina up to the cortex is thus known to us as regards its general direction, and even as concerns its multiple paths of return towards the periphery, as will be explained farther on. In proportion to the progress made by it in the deep portions of the system, it undergoes divisions or predetermined orientation in the more and more numerous paths opening out before it. The reflex arc, which is the form taken by the journey as a whole, not only presents gradations, but also undergoes interruptions in its length ; these, however, not being total but segmentary, and more numerous as the cortex is approached, towards and in which everything attains its maximum of complexity. The pulvinar, the geniculate body, the corpus quadrigeminum all correspond to breaks of this nature, destined for the adaptation of the luminous and visual impulse to its very varied functions. They are analogous, but not identical parts, and thus cannot completely supply each other's place. Of these three grey masses, the

one most essential for the transmission to the cortex of luminous impulses is the geniculate body (Gratiolet).

The cells of this ganglion are so arranged that, for the most part, their axis cylinders are orientated towards the brain, thus indicating that the progress of the impulse proceeds from the geniculate body to the cortex (Monakow).

We are unacquainted with the existence of any fibres bringing back the impulse from the geniculate body towards the motor periphery; this, however, being assuredly no proof of their non-existence. On the contrary, we know of some which, from the other ganglia, and especially from the corpus quadrigeminum, reflect the impulse on the motor organs; for example, the irido-pupillary reflex.

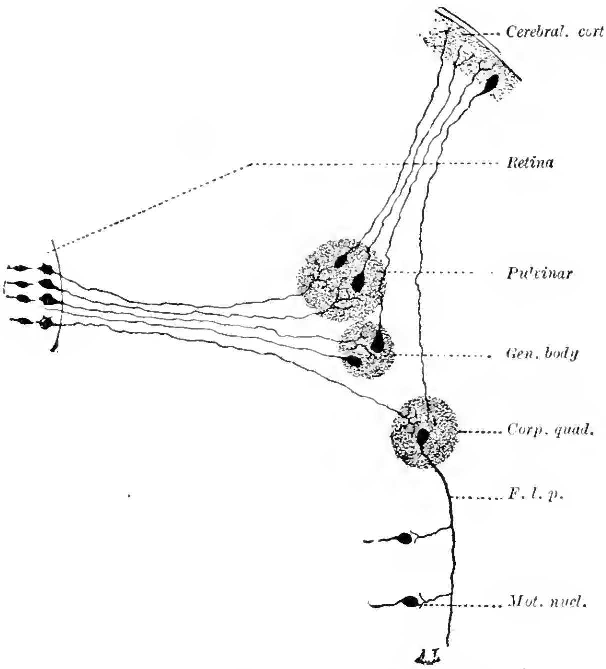


FIG. 230.—Ganglionic optic paths (diagram).

Functional and evolutional balance.—If we examine the *development of the grey sub-cortical masses in the vertebrate series*, it will be seen that this development *is, as regards some, in inverse ratio to that of the cortex, and as regards others, in direct ratio to its development.* Specifically, the bigeminal tubercule (optic lobe) follows the first course; the external geniculate body and the pulvinar follow the second (Edinger, Forel, Monakow). The quadrigeminal, or bigeminal tubercule (optic lobe), forms one system; the cortex of the hemispheres, the pulvinar, and the geniculate body form another. The first is the oldest of these two systems: that is to say, that it can exist alone, and discharge (with the similar organs of the other senses) the rudimentary psychical functions of inferior animals; it is thus that in certain fish the pallium does not yet exist, and is represented by an epithelial layer which covers the ventricles. The second, in proportion as it is more highly developed, and as intelligence takes the place of instinct, deprives the former of its functions (whence arises atrophy of the optic lobes, which are replaced in mammals by the corpora quadrigemina), and becomes augmented both in its cortical and ganglionic portions (whence the development of the pulvinar and the geniculate body in mammals).

In reality this division is not so markedly schematic inasmuch as a portion of

the optic thalamus, and even of the geniculate body, appertains to the first system (primary system, whose function is reflex). As the intellectual system develops it reduces a portion of this whole, principally the bigeminal tubercule (optic lobe), while it increases the other portion (optic thalamus and geniculate body) by the prolongations which the pallium conveys to it through its own development.

The study of degenerations also supports this conception. After the removal of the cortex all these masses display degenerated fibres alongside of healthy ones, but the relative proportion of the two is then very different. The anterior corpus quadrigeminum remains almost healthy, but the optic thalamus shows extensive degeneration at the level of the pulvinar, and the external geniculate body is almost completely invaded by this degeneration.

Functional distinctions.—By the help of the actual information afforded us by physiology and clinical surgery, an effort has been made to establish functional distinctions between these three morphologically remarkable grey masses—the anterior corpus quadrigeminum, the optic thalamus, and the external geniculate body; and, with this end in view, the following differences are brought forward. The first of these centres is purely *reflex*, and it throws back the impulses it has received on to the intra-ocular or peri-ocular muscles. The second is a centre for reflexes of *instinctive* order, by which emotions are revealed (movements of the eyes and the face, mimicry expressive of the emotional sensations received by the eye). The third, unlike the two others, instead of bringing back the retinal impulses directly to the motor paths, on the contrary, involves them still more deeply in the brain, and by the optic radiations conveys them to the cerebral cortex, where they give rise to distinct *sensation*, to the formation of an image, and finally to the *idea* preserved in a state of remembrance before being revealed by a motor act.

Isolated lesions of these three grey masses, if it were possible to realize them or to meet with them absolutely localized, would be rendered evident by the isolated abolition of each of these three forms of reaction, namely, as regards the corpus quadrigeminum, loss of the inferior reflexes; the optic thalamus, that of emotional expression; the external geniculate body, loss of the capability of awakening visual sensations, but at the same time with conservation of the images and ideas previously formed, so long as the visual cortex, with the connexions uniting it to the other senses, is still preserved.

Comparative visual physiology.—This classification is not applicable as such to the whole series of the vertebrata. The lower we descend in the scale the greater is the importance assumed by the sub-cortical centres relatively to the cortex, whose functions they more or less share. Conversely, the higher we ascend the more we see the cortex monopolizing the functions of these grey masses, but at the same time differentiating and improving them in a singular manner. At the summit of the series many purely reflex acts have become instinctive, and instinctive acts intelligent. The organs subserving reflex and instinctive acts persist, but they discharge less important functions, and this not merely from a relative, but also from an absolute point of view.

B. THE RETINAL IMAGE. RODS AND CONES

The longitudinal cleavage of the visual system begins at the surface of the retina which receives the luminous excitations. In fact, the retinal field is divided into two very unequal portions: one central, being the *yellow spot* containing the *cones*; the other peripheral, containing more especially the *rods*.

1. Functional differences.—Max Schultze, owing to certain indications yielded by anatomy and comparative physiology, believed that the rods are connected with luminous perceptions and the cones with the perception of colours. Parinaud has rendered this connexion more precise, and has studied the mechanism of these functional differences. The *human retina*, he remarks, is formed as it were of *two associated retinæ ;* that of the *cones* and that of the *rods*. The former yields the sensation of light and darkness ; and, further, all the colour sensations. The second only supplies the sensations of light and darkness ; from this point of view it is less perfect than the preceding, but this imperfection is compensated by another quality. As twilight approaches, or when darkness is artificially procured, this retina containing the rods has the power of *adapting* itself to a very feeble illumination and enables us to recognize the objects around us. In *hemeralopics* who have lost the power of seeing in a feeble light it is this retina which no longer fulfils its function. As v. Kries has also observed, the cones are an apparatus adapted for strong light, and the rods for partial obscurity. In total daltonism (congenital) the opposite is the case ; the cones being impaired, the perception of colours no longer exists, but as the rods are intact the perception of light is still preserved.

Retinal visual purple.—The rods are found almost exclusively in the retina of nocturnal animals (owls, bats, hedgehogs) ; in most birds the cones predominate or are alone present. The adaptation of the perimacular region of the retina, or of the rods, to very feeble illumination must be connected with the presence of the retinal visual purple, or *rhodopsin*, which is absent in the macular retina or the cones. This substance, which is easily decomposable by light, is fluorescent, or, in other words, it absorbs certain rays, principally the invisible chemical rays, and transforms them into visible rays, thus augmenting the illumination of the retina.

The region of the macula lutea possesses one other function which distinguishes it from the area surrounding it. The *image of the objects* we are looking at is thrown on the *fovea centralis*, and this image is here more distinct than in the rest of the retina ; the absence of visual purple, and therefore of fluorescence, helps to give it this distinctness. Thus the cones play the principal part in the performance of the retinal functions, possessing as they do the faculty of differentiating luminous impressions which are geometrically distinct, whence results the perception of forms, or *visual acuity* properly so called (Parinaud). It must also be observed that each cone is connected with a bipolar cell, while each bipolar cell is connected with several rods. In the yellow

spot, the cones are not only solitary, but are also very small and closely pressed against each other; their diameter is about 0·002mm. to 0·0025mm. (Schultze). But the shortest distances between two retinal images which can be distinguished from each other are from 0·0043mm. to 0·0054mm. (E. Weber, Helmholtz), or, by practice, 0·003mm. (Volkmann), this figure approaching that of the diameter of the cones and, by comparison with it, explaining to us the limits of distinct vision.

2. **Macular and peri-macular tract.**—The *fovea centralis* is connected with a distinct tract of the optic nerve, which may be followed along the whole course of the latter. This is the macular tract, and a section of the optic nerve (near to the ball of the eye) closely resembles the arrangement which holds in the retina and its division into two areas, the one central and the other peripheral, both having distinct attributes.

3. **Direct and crossed tracts.**—This being allowed, it is found that, from another point of view, the retina and the tracts of the optic nerve arising in it, present a second division which is effected in the following manner: each of the retinæ of the right and left eye is itself divided into a right and left portion, mutually unequal (two-thirds on one side and one-third on the other), by a vertical line passing through the *macula*. That portion of the optic nerve which corresponds to the temporal area proceeds to the cerebral hemisphere of the same side; that corresponding to the nasal area decussates in the chiasma with its homologue in order to reach the hemisphere of the opposite side. This decussation affects the macular tract as all the rest. As regards each eye, the term *nasal* is applied to the inner area (with reference to the median line of the body) and *temporal* to the external area; the nasal area is the most extensive of the two.

4. **Corresponding areas; identical points of the retina.**—Though the nasal and temporal areas correspond with each other from the point of view of ordinary symmetry, the same cannot be said with regard to the normal exercise of vision with both eyes. An object placed to the right throws its image on the two left areas of each retina, an object placed to the left on the two right areas. Thus each point of the object throws two images, one on each right or left area of the two retinæ. These points, which are called corresponding or identical (J. Müller), are mutually united by the nervous system in such a way as to cause these two images to be fused into one in the sensorium. These points being once fixed, it is necessary for the exercise of normal vision that they should continue in the same mutual relations as regards distance during every movement of the eyes.

5. **Homonymous hemianopsia.**—Should the optic nerve on one side be interrupted, loss of vision in the corresponding eye would naturally

ensue. If the optic tract of this same side is interrupted, there is loss of vision in each of the corresponding half retinæ, the temporal on the same side and the nasal on the opposite side. This is called homonymous hemianopsia, because the two half retinæ deprived of sight are those of the side corresponding to the lesion. In other words, the two temporal areas give off direct fibres (connected with the hemisphere of the same side), the two nasal areas give rise to decussated fibres (in relation to the opposite hemisphere) ; or, to put it otherwise, the two right areas of each retina are connected with the right hemisphere, the two left areas with the left hemisphere. Grasset remarks on this subject that the optic nerve only exists as a physiological unit in the optic tract, and that in strictness it should be described as the *hemioptic nerve.*

Remark.—If a hemisphere is injured or the optic tract interrupted, it is the half retinæ of the same side which are paralysed, but the objects on the opposite side are those which are no longer seen. This is explained very easily by the fact that the images of these objects are reversed on the retina on account of the passage of the rays through the media of the eye. This disappearance of sight to the right or the left in the case of experimental or pathological lesions of one or the other hemisphere has given rise to the belief which for some time prevailed that the sight of the right or the left eye was paralysed in an isolated manner, and as a finishing touch to this error, that the paralysis affected the eye opposite to the lesion. By closing each of the eyes separately, it is easily seen that the sight in each is partially preserved and partially extinguished, according to the above-mentioned division.

Decussation of fibres in the chiasma.—Since the time of Newton, who first considered the question, the decussation, whether partial or complete, of the optic nerve has been continually discussed. In inferior vertebrata we find the eyes placed laterally and the vision monocular; in them the decussation is complete. Even in mammals, examples of total decussation may be found: for instance, in the guinea pig and the mouse : it is partial in the rabbit, the dog and the cat ; in the primates it is much the same as in man. In the last named the proportion of fibres would be 150,000 direct to 250,000 crossed (Krause, Salzer).

Experiment.—Nicati, after having cut the chiasma of the optic nerves in the median line, across the bones of the base of the skull, in a young cat, observed that vision partially persisted in the two eyes, this proving that a certain portion of the fibres escape decussation.

Amblyopia by sensory anæsthesia.—The isolated lesion of a hemisphere never produces crossed amblyopia or hemiopia ; but constantly causes bilateral homonymous hemianopsia. Unilateral amblyopia or hemiopia may be observed as a natural consequence of the interruption of the optic nerve, but it may also have a more complex origin. Clinically, an amblyopia of this nature generally arises in connexion with an anæsthesia of the ball of the eye. It may be observed in hysteria, when it occasionally causes a very marked contraction of the field of vision, and it only occurs when there are contemporaneous disturbances of general sensation which affect the ball of the eye, and it is more marked in proportion to the strength of these disturbances (Ferré). It may be reproduced experimentally by inducing lesions of the nervous system en-

tailing anæsthesia, whether these lesions have a central cortical origin (Lannegrace), or whether they are, on the contrary, peripheral, or equivalent to peripheral lesions (Bechterew). It may, in fact, be induced by section of the trigeminal, especially of its ascending root. The sensory anæsthesia which ensues in the corresponding half of the face is accompanied by a diminution in the acuteness of the senses (hearing, smell, taste), as has been pointed out by those who have experimented on section of this nerve.

Thus the sensorial disturbances following the paralysis of this nerve are of a secondary nature. Section of the trigeminal nerve interrupts not only sensory fibres, but also vaso-motor elements, and probably also elements whose function is of a more indeterminate nature, and whose interruption is rendered evident by trophic disturbances. In all cases the section is followed by disturbances of nutrition, which explain the diminution or lack of function of the sensory organs situated in its area of distribution.

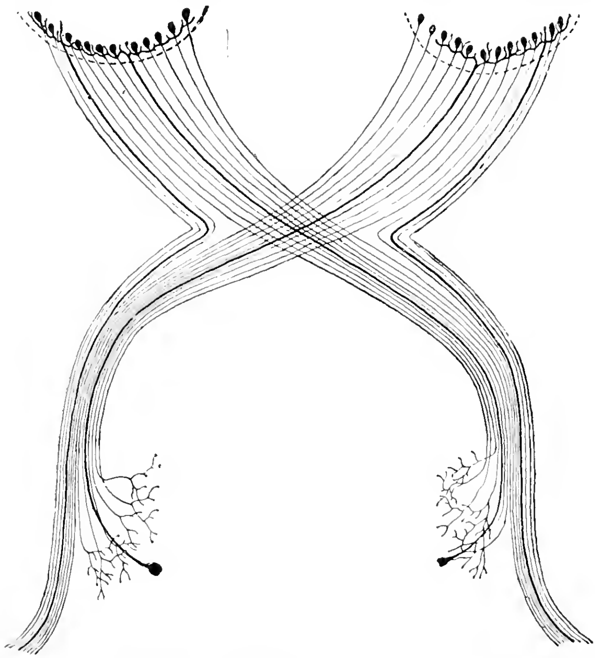


Fig. 231.—Diagram of the structure of the optic nerve (after Van Gehuchten).

6. **Persistence of the retinal impressions.**—The impression made on the retina by a luminous excitant persists for a certain time after its cessation. The most simple illustration of this is afforded by a red-hot coal which, if moved in a circular direction, gives the impression of an incandescent circle. The cinematograph is founded on this fact. This persistence varies according to the intensity of the light emitted by the object which stimulates the retina. Helmholtz has observed it to vary from $\frac{1}{48}$ of a second in the case of very brilliant to $\frac{1}{20}$ of a second in that of feeble illuminations; $\frac{1}{50}$ of a second would be a maximum figure, impossible to go beyond, and, indeed, hardly to be attained even with the strongest illuminations (Parinaud).

Consecutive images.—When the more or less persistent primary image has ceased and the eye is suddenly plunged into darkness, a consecutive image, which has been named *positive*, makes its appearance after a short time; this name has been given it because it reproduces the first image without inverting

its tones (white for white, black for black). This image is progressively effaced, and after a time, which may vary from a second to a minute or longer, it is usually replaced by a *negative* image, in which the tones are reversed (black for white, or the colour which is generally complementary instead of the primary colour). The negative image may not appear when the first impression has been a feeble one.

Retinal oscillations and interferences.—Thus a luminous stimulation has both immediate and consecutive effects. When studied in detail, both will be found to be complicated. The immediate impression is itself an effect of an oscillatory nature. A. Charpentier maintains that *all luminous stimulation* (whatever be its colour and intensity) *gives rise to a negative undulation in the retina*, probably followed by other oscillations analogous to it, but which are less easy to observe.

(*a*) *Oscillation arises in a stimulated point* $\frac{1}{60}$ to $\frac{1}{70}$ *of a second after the commencement of the stimulation;* the period of complete oscillation being from $\frac{1}{30}$ to $\frac{1}{35}$ of a second. (b) *This oscillation, starting from the excited point, extends gradually on the retina at the rate of* 72 *millimetres the second.*

Experiment.—A black disc carries a white well-lighted sector, and is caused to rotate on its axis at the rate of one turn in two seconds. The eyes must be immovably fixed exactly on the centre of the disc. A black sector, with a softened outline, is seen to appear, covering a portion of the white sector. If the rate of rotation be increased, this black band becomes larger; should the rate be diminished, it decreases in size. By calculating the rate of rotation and the distance separating the black band from the border of the white sector the interval which has elapsed between the appearance of the white edge and that of the black edge arising on it may be deduced. This interval is $\frac{1}{60}$ to $\frac{1}{70}$ of a second.

Charpentier maintains that the negative wave answering to this black band travels successively over the different meridians of the retina. It always arrives $\frac{1}{60}$ to $\frac{1}{70}$ of a second after this point has been touched by the beginning of the white sector.

The starting of the stimulation produces an oscillation at the point stimulated. The duration of the complete oscillation being from $\frac{1}{30}$ to $\frac{1}{35}$ of a second, after from $\frac{1}{60}$ to $\frac{1}{70}$ of a second the oscillatory phase is negative.

The fresh excitation (of a positive order) is superposed to it; hence arises interference, opposition of contrary movements, and thus darkness ensues: $+\Delta + (-\Delta) = 0$.

The study of the excitability of the retina will be resumed in detail with regard to the functions of the organs of the senses. What we have stated above merely indicates that, starting from the retina, the phenomenon of visual stimulation is one of great complexity, and cannot be explained by a simple transmission of a nervous impulse through isolated fibres. From the retina there is a tendency to the diffusion of the impulse in an area near to the point directly stimulated. The distinctness of the psychical image is no longer, like that of the physcial image, determined by the existence of a geometrical arrangement which continues across the optic paths up to the cerebral cortex.

7. Unity of sensation in binocular vision.—In binocular vision the two physical images formed at the back of each eye are fused into a single psychical image. This synthetic phenomenon is in reality not more surprising than are many others from which our sensations and perceptions result; but it is here more obvious, and strikes us more forcibly on account of the distinct separation between the elements

by which the sensation is perfected. An attempt has been made to explain this by observing that the impressions received on the homonymous areas, that is to say, the right and left halves of the two retinæ, converge by means of the optic tracts and the optic radiations towards the same cerebral hemisphere, in which are thus superposed nervous waves of the same form and the same succession. But this is only a part of the explanation ; it remains to be shown how these psychical images formed in the two hemispheres are, in their turn, superposed so as to form a single image. To effect this the inter-hemispherical commissures must take part, the most important of them being the corpus callosum, which solidarize the functions of the two halves of the brain. We relapse into the formula common to all sensation ; a phenomenon which in itself and by definition ensures unity, but whose physiological analysis displays component elements, proving them to be the more dissociated the farther they are removed from the cerebral cortex.

Further, it must be remarked that the right and left areas of the two retinæ are not those which play the most important part in vision, but rather the central area, or that of the yellow spot, placed on the line of division between the preceding. It seems often to be maintained that the yellow spot is itself divided by hemianopsia into two halves, one being insensitive and the other sensitive. According to Monakow, disturbances localized in one hemisphere would, on the contrary, respect the macula lutea in great measure, while they would suppress vision in the homonymous areas of the periphery. An attempt has been made to explain this fact by assuming that the macula of each side is united to the two hemispheres at the same time, or else by maintaining the evidence of a cortical localization of the impulses from the macula which would be different from that of the rest of the retina. Monakow, on the contrary, thinks that its cortical territory is much more diffuse, and that herein lies the reason of its comparative escape from paralysis.

However this may be, the image of an object placed directly before the eye and formed in the centre of the macula is, as it were, astride fibres which, being partially crossed like the others, project it on the two hemispheres, the synthesis of the object being still made in the sensorium.

C. CEREBRAL VISUAL SPHERE

One portion of the area of the cerebral cortex is devoted to vision. The visual sphere, as Munck calls it (and this designation is incontestably more correct than that of *centre*), is situated on the surface of the occipital lobe.

1. Former experiments and observations.—Gratiolet in 1854 discovered the optic radiations and followed them from the basal ganglia, and especially from the external geniculate body of which he perceived the great importance, up to the cortex of the occipital and parietal lobes. Panizza, in 1855, observed the unilateral and crossed blindness which follows the removal of the posterior convolutions of the brain

or lesions of the white fibres uniting them with the basal ganglia ; when the lesion is bilateral, the blindness is complete, but the other functions are preserved. He also noticed the ascending degeneration of these tracts, and of their ganglia of origin, in the case of loss or removal of the eye. The error which led him to believe in unilateral blindness, implying a complete crossing of the optic nerves, was generally diffused, and was only rectified much later, and after much discussion. It is also explained by the usually preponderating importance, especially in animals, of the crossed tract over the other, and also by the direction which it is necessary to give to objects in order that their image may be thrown on the retina. The objects placed on our right are seen by the left halves of the two retinæ, and conversely for those situated on our left.

2. **Cuneus and calcarine fissure.**—Physiology and clinical experience are quite agreed with regard to the localization of the visual sphere of the cortex on the internal surface of the occipital lobe, in an area chiefly comprehending the calcarine fissure. Some authors have considered this area to be limited to the lips of this fissure only (Henschen), others (Monakow) that it extends as far as the three convolutions of the external surface of the occipital lobe, and that it even encroaches on the posterior portion of the parietal lobe. Most, however, regard it as being restricted to the internal surface of this lobe (Bouveret) ; it essentially includes the cuneus and a portion of the lingual lobe, that is to say, the two convolutions forming the boundaries of the calcarine fissure (Dejerine, Vialet, Brissaud).

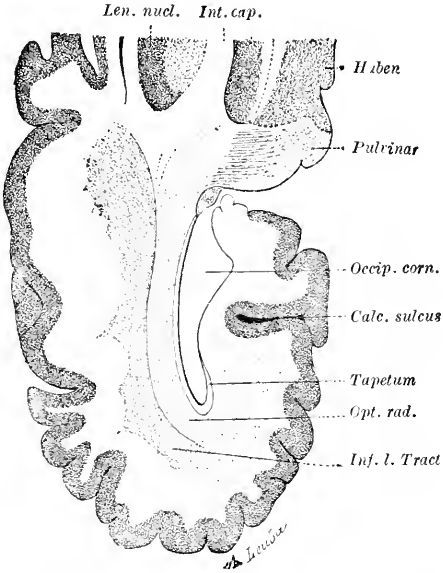


FIG. 232.—Optic radiations and occipital lobe.

Horizontal section of the left hemisphere (after Charpy).

In animals the cortical visual sphere has, by the experiments of Munck, been located in the occipital lobe.

Vitzou has observed *unilateral ablation*, total and simultaneous, of the posterior third of the first, second and third parallel convolutions of the *occipital lobe*, to be followed, in the dog, by *bilateral homonymous hemianopsia.* Blindness affected three quarters of the retina of the opposite side, and a

quarter of the retina of the same side. The decussation of the optic fibres in this animal was therefore effected in the proportion of three fourths to a fourth.

Lesions of the angular gyrus.—Experimenters and observers have, nevertheless, pointed out the *pli courbe* or *gyrus angularis,* situated on the external surface of the brain, as being the cortical centre of vision. Their error is explained by the anatomical fact that the optic radiations, in their journey from the basal ganglia to the occipital lobe, pass slightly below the cortex of the angular gyrus and are easily cut or compressed by changes affecting the latter.

Stripe of Vicq d'Azyr.—(*Ruban de Vicq d'Azyr.*) Differences in form, structure and arrangement of elements lead us to suspect differences of function, and this even when the mechanism of these functions is unknown to us. It has been noticed that the structure of the cortex of the calcarine fissure slightly differs from that of the neighbouring cortex of the occipital lobe ; the difference consists in the greater thickness of the molecular layer, and also in the development of a band of horizontal fibres, the stripe of Vicq d'Azyr (ruban de Vicq d'Azyr).

3. **Surface of projection.**—Several authors call the visual sphere a "cortical retina," intending by this appellation to point out that each point of the retina is united to the cortex by conducting fibres, whose terminations in it repeat on its surface relations analogous to those which they mutually possess in the ocular retina. But they cease to be in agreement when the question of defining these relations arises ; and it must be admitted that facts are wanting, both as regards number and value, not merely as concerns the arrangement in detail, but also to guarantee the principle.

Geometrical projection on the cortex.—Thus, for example, in a case of atrophy of the superior lip of the calcarine fissure, the occurrence of a hemianopsia, limited to the lower quarter of the visual field on both sides, has been recorded (Hun). In a similar case, but one in which the lesion occurred on the inferior lip of the same fissure, a hemianopsia of the upper quarter of the visual field has been noticed (Wilbrand). Yet the localizations of the macular and marginal portions would not possess the concentric arrangement which they have at the back of the eye, but the first would be at the anterior and the second at the posterior portion of the calcarine fissure.

Objections.—We must repeat that these localizations require confirmation. Monakow has challenged the principle, supporting his objections by numerous facts showing the physiological importance of the intermediate ganglion (the external geniculate body), which interrupts the continuity of the conducting elements, so that they cease to be visible in the shape of unbroken fibres, whose extremities would be spread out over two opposed surfaces : that is to say, the retina and the occipital cortex. The grey matter, wherever existing—and this we know from a hundred examples—creates associations, and therefore new relations, between the conducting paths arriving in it and those which leave it. An accurate projection of the retina on the cortex is not only not demonstrated, it is also improbable.

Composite projection.—That which is called projection on the cortex is, in

fact, a perfectly ordered, but extremely complex, shock, affecting the cyclic visual system both in breadth and in depth according to laws of which we are ignorant. One necessary condition is evident, namely, that, for similar images, this shock must be regulated in a similar manner and for different images in a differing manner. But the simple conditions as regards the formation of the retinal image are no longer those which preside over the formation of the cerebral image, itself giving rise to the psychical image. When the retinal image changes its place on the retina, it is indeed probable that the cerebral image also changes its place in the cortical sensorial field ; but this phenomena of the localization of the cerebral image is distinct from that presiding over its production.

Limits of the visual sphere.—Nothing is more undecided or more difficult to define than the limits of the cortical area which appertains to vision, though in point of fact the same may be said with regard to all the other senses ; and nothing is more deceptive than any attempt to trace these limits in a hard-and-fast manner. In fact, if each of the senses is rigorously localized at the periphery of the body in special apparatus only adapted to distinct varieties of shock, it is not so in the brain, and especially not so in the cortex, whose function it is, not merely to collect these impulses, but to put them in conflict with each other, so as to extract the elements of knowledge from them, and finally to send them forth under the form of motor activity.

Discordant evidence.—Distinct vision has sometimes been preserved in an extremely small visual field (for example, an extent of from only 3 to 5 degrees around the point of fixation), which still allowed the patient sufficient visual acuity to read or to occupy himself with different kinds of work : the occipital lobe showed very extensive areas of softening, with preservation of certain very limited portions of the cortex of the calcarine fissure. But the observers by whom the facts were confirmed disagreed concerning the localization of this portion of the grey matter: according to Henschen, it is in the anterior portion of the fissure, but according to Forster and Sachs in the posterior portion. Henschen thinks that there is a surface dissociation of the centres corresponding to the yellow spot and to the margin of the retina ; but Munck is of opinion that there is exact projection of the ocular retina on the cortex, and therefore a concentric arrangement of the two centres.

4. **Luminous sensation and mental vision.**—Before endeavouring to delimit the anatomical area of the visual sphere, it will first be necessary to define what is exactly implied by vision. From crude sensation of light or of colour up to mental vision a graduated field of phenomena exists, each effected by functional nervous associations which are definite in their determinism, but variable according to each modality of the phenomenon. These are the gradations which more or less extensive destructions of the cortex may sometimes bring into notice, unless they are of too delicate a nature to be grasped.

Cortical retina.—The expression *cortical retina* has practically merely a metaphorical signification. As opposed to the locality where the impression of light

which is at first purely physical, has been received, it implies another locality, where this impression, after successive transformations, has given rise to the psychical phenomenon of sensation. If this expression be retained, it must in no case be considered as being the equivalent of "visual sphere": the cortical retina would imply the field of visual sensation, while the visual sphere would correspond to the field of mental vision, both of them possessing undefined and indeterminate limits.

5. **Different forms of blindness.**—It is possible to be blind to white light and to colours at the same time; and it is also possible to be blind to colours only. This limited blindness may appertain to all colours (*achromatopsia*), or only to some special ones (*dyschromatopsia*). In the case of unilateral cerebral lesion, there will be *hemiachromatopsia*, or *hemidyschromatopsia*.

Conditions of their production.—On the surface of the retina (at the starting point of the impulse), the chromatic function is localized in special elements (the cones) different from those which are sensitive to light without distinction of colour (the rods). In the retina, colour vision is central and vision apart

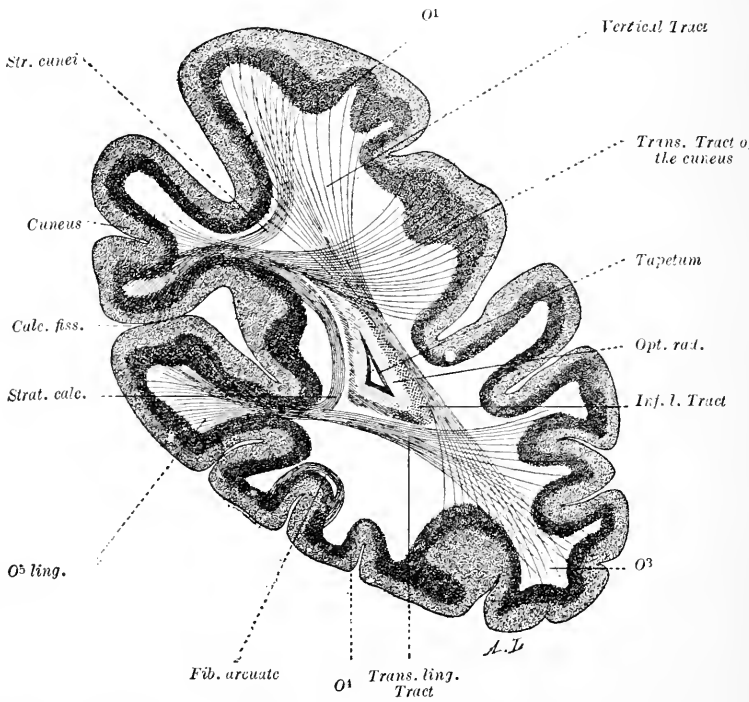


FIG. 233.—The tracts of association of the occipital lobe.
Diagrammatic transverse section.—Left hemisphere (after Dejerine).

from colour is marginal. Is it the same in the cerebral cortex? Nothing indicates this in a definite manner, and probability is not in favour of such a symmetry. On the other hand, to mark out a cellular layer devoted to the colour sense in the cortex of the grey occipital matter, is to bring forward an

absolutely gratuitous and unverifiable hypothesis, since there is no chance of finding or artificially producing a lesion affecting preferably one cellular layer to the exclusion of others. With regard to surface localization, so much is still wanting that clinical observations followed by autopsy do not authorize our acceptance of it.

Some prefer to maintain that colour vision is not distinctly localized apart from that of light, but that it merely depends on certain special conditions, such as a very perfect preservation of the irritability of the elements and an adequate blood supply; or, again, on a more extended visual field. In the case mentioned by Forster, in which the visual field was extremely restricted, there was colour blindness. Cerebral lesions, according to their intensity or their extent, would thus cause, in the first place, loss of the sense of colour (the most fugitive); then that of the sense of light; lastly, complete blindness. Green and red are the first to be lost; then blue; and finally, the conception of black and white (Holden). In general the appreciation of various intensities of light continues to decrease with that of colours, though in the end surviving it; but clinical observation, which teaches us so much, brings forward a case where loss of colour vision occurred without diminution of sensibility to light (Stefan), and this case is quoted as an argument by those who maintain the independent existence of a centre for chromatic vision; but there is nothing convincing about it.

6. **Conceptions of form, space, locality and of orientation.**—To the simple conception of light, and to that more complicated idea of colours, are added, in the exercise of vision, other notions which are generally so strictly associated with each other that they are only distinguishable by analysis; these are the ideas concerning the form of objects, and the mutual relations of these objects, as well as those with ourselves. These ideas are far more complicated than the preceding ones. By the combination of light and shadow as well as colours, images are formed on the retina. These images are brought into being by association in a given order, that is to say, by the synthesis of these elements (luminous and chromatic phenomena). This synthesis is a psychical fact. Each of these elements exists independently; their association in our consciousness is what gives the image its reality.

7. **Physical image and psychical image.**—Physics teaches us how luminous rays emitted by objects or reflected by them, while preserving their respective relations, may, when falling on a screen, furnish a representation which exactly recalls these objects, and which is of about the same dimensions. This is what is known as the *physical image* of these objects. It is by an image of this nature that objects make an impression on the retina, and this image is as much a physical one as that which was thrown on the screen. But the retina possesses, as the screen does not, nervous paths which carry this impression into the depths of a system whose strictly consolidated parts form a really united being, and this unity is revealed in it by that which we call consciousness. In this case the physical image is duplicated by a

psychical image, or, to put it better, the consciousness, by arranging the characteristics of the physical image, and at the same time detaching it from all surrounding phenomena, confers upon it its unity, that is to say, its existence. This is not the appropriate place for explaining the manner in which, from the retinal image, we ascend to the objects.

8. Empty space and occupied space.—Whatever the reason may be, it seems that even from the fact of their original complexity, these conceptions of form are more easily alterable than the elementary sensations which gave rise to them. It has been observed that, in double lesions of the occipital lobe, individuals injured in this way lose the faculty of recognizing localities which should be familiar to them. The general idea of space may be preserved, but that of space furnished with objects no longer exists with its characteristic attributes for these patients: they have lost the memory of localities.

An endeavour has been made to find in the occipital cortex, both in its depth and on its surface, a special centre of visual acuity and of vision in space; but here again, facts are wanting which would serve as a basis for such a conception, which no satisfactory theoretical reason suggests to us. What appears to be certain is, that *the cerebral field whose activity presides over recognition of forms and places is more extensive than that for the crude sensation of light;* the nervous apparatus of the one differs from that of the other, just as the first of these phenomena differs from the second, or just as the composite differs from the simple.

Exteriorization of sensation.—Objects are situated externally to us, and we have a knowledge of their existence: it must therefore be that something comes from them to us, carrying with it the elements of this knowledge. The aërial medium and especially the ether (this last penetrating all the others without being confounded with them), carries out this transmission as regards objects at a distance. Something which has, as it were, taken the impress of these objects thus comes to us and reconstitutes this impress on the sensory surface of our body; this is very evident with regard to the sense of sight.

This impression, however, has not finished its progress by its arrival at the retina; it travels thence by quite new and special paths (the nervous paths), in order to reach the cerebral cortex; there alone does this imprint or this impression become sensation, perception, or knowledge. This amounts to saying that the imprint, the image, exists in us, but the medium containing it (and this medium is ourselves) is conscious of so doing. The external medium which transmitted it to us (it, or its component elements) also contained it, but without the consciousness of doing so. These facts are individually clear, and arise from common sense and from intuition. One of them, it is true, namely, consciousness, eludes all rational and scientific explanation, and will probably always so elude it, on account of our special situation with regard to it. However, for the present it will suffice to authenticate it and put it into its right class.

At the same time, this is only half the explanation. The forward march of the impression (or of what produces it) from the objects to us explains clearly

how their image comes to exist in us, but it does not explain how these objects are collected externally to us in the locality which they really occupy. The fact is authenticated and connected with the preceding datum by saying that the sensation, the mental image, is projected externally in the direction and even to the situation of the object. This is what is called *exteriorization of sensation.*

These words, *exteriorization* and *projection*, are necessary to complete the analysis of the process of formation of the mental images of objects. They express a correction which is in a way indispensable in order to bring the results of this analysis into agreement with common sense. In fact, on the one hand analysis evidently displays to us something which is substituted for the object and which progresses in the first instance from it to us, then within us up to the brain: as if this object had come to dwell there and to manifest its presence by some of its characteristics. But, on the other hand, common sense is not deceived, and locates these objects where they really are, outside of us, that is to say, externally to ourselves: so that, after having caused this something which represents the object to travel from it to our brain, we feel, for the sake of logic and good sense, the necessity of requiring it to perform the opposite journey, that is to say, from our brain back again to the object. To put it concisely, there would be: (1) projection from the object up to the brain; (2) projection from the brain to the object. What is this something which is launched on both of these journeys? From the object to the brain the projection is a reality, and is itself divided into two successive journeys; these are, from the object to the retina, luminous waves propagated through the ether, obeying laws which are fairly well understood; and, from the retina to the brain, nervous waves, of which the direction of the propagation (if not the form) is distinctly defined.

On the contrary, the projection from the brain to the object is quite ideal; it is merely an artifice made use of for the purpose of demonstration. It is the same thing as saying that physical and physiological analysis of the mechanism of vision only gives us a portion of the knowledge necessary in order to arrive at a clear conception of it. In any case there is no such thing as a nervous retrograde wave which returns from the brain to the retina by paths already traversed by it on its journey from the retina to the brain. Doubtless it would be possible for the brain to reflect these waves, and thus project them outwards, but it would be by paths quite different from the first, and which would bring back these waves to the organs of movement, where finally all nervous impulses terminate.

9. **Physical and psychical blindness.**—Nothing can be more instructive from a psychological point of view than the comparison of two individuals, of whom one has lost the ocular apparatus (loss or ablation of both eyes) and the other the cerebral apparatus of vision (pathological destruction of the occipital cortex or ablation of the occipital lobes). Experiment and observation, which so often leave questions undecided because they are impracticable in conditions which would render them precise, here find a field favourable to their realization by attacking the two positions of the visual system which are the widest apart, and by comparing the deficiency which follows, in the one case the suppression of the receptive apparatus, that is to say, the original source of impulses; and in the other, the suppression of the essential mechanism for the transformation and preservation of these impulses.

The subject, whether it be man or animal, which has lost both eyes, no longer receives any ideas from the external world by the visual path, but preserves in the condition of remembrances a great number of those previously acquired by this means, and which remain in him in the form of so many fixed data round which to group the new ideas which do not cease to flow in upon him by the paths of the other senses still remaining intact. The individual, on the contrary, who no longer retains the occipital lobes has lost with them the accumulated store of anterior ideas acquired by sight; therefore the information brought by touch, hearing and smell will no longer have as a basis the memories acquired by the sense playing the most essential part in the representation of forms and places; owing to this fact a very great mental inferiority will be observed in the second case when compared with the first. Both subjects are plunged into obscurity, but the night of the first is a *physical night*, not essentially different from that resulting from a simple deprivation of light, understood as vibrations of the ether in the physical sense; the night of the other is a *psychical night*, in the sense that the vibrations of the ether may indeed affect the retina, and by reverberation the primary visual paths; but light in the physiological or psychological sense of the word (the meaning is the same), is lacking; while in the first even this light is not absolutely extinguished, and still less so are the forms impressed on the consciousness.

In physical blindness the other senses, and especially that of touch, soon become sufficiently educated to allow of their supplying to a certain extent the absence of vision; this education being possible, thanks to the nucleus of visual memories preserved in the brain. In psychical blindness this education finds its principal basis lacking, above all in the adult. The child born blind, or the new-born animal, from which both eyes have been removed, would also be forced to create a tactile and auditory sense by the education of the remaining senses; but their condition would be ameliorated by reason of the greater plasticity of their organs still in course of development.

10. **Verbal blindness.**—The word "psychic," like many expressions used in physiology, may be understood, sometimes in a general and sometimes in a special sense, and, until our language is enriched with expressions adequate to describe these shades of meaning, it is better to define them by short descriptions. Psychical blindness, when understood in the sense just referred to, is equivalent to the loss of all psychical phenomena of a visual order, from the crude sensation of light up to ideas of a most complex nature, in so far as these proceed from vision. *Psychical* is thus taken simply in an opposite sense to *physical*.

We may thus define the principal degrees of this psychical phenomenon.

It is usual also to distinguish ; (1) a *cortical* blindness, equivalent to the loss of luminous sensations ; (2) a *psychical* blindness, properly so called, equivalent to the loss of commemorative images of objects ; (3) a *verbal* blindness, implying the loss of the power of reading words, or, more generally, any written signs. This last variety is included under the heading of aphasia.

Inferior psychism.—Visual images are projected on the cortex ; but, before reaching it, they pass through the optic thalamus (pulvinar) : this ganglion takes an active part in the elaboration of visual sensation. After the removal of the cortex of the occipital lobes, blindness ensues, but after a certain time this blindness is ameliorated (Munck), exactly as is the sensory paralysis following the ablation of the tactile cortical area. The animal, in walking, succeeds in avoiding obstacles. There must then be some recovery of visual sensation with a certain degree of consciousness. The permanent deficiency which follows destruction of the cortex is not then characterized (at least in animals) by absolute loss of conscious vision, but by the impossibility of elaborating complex images. As for the return of conscious elementary vision, when this re-appears, there is nothing which would compel us to consider it as caused by a substitution of neighbouring portions of the cortex which have remained intact, rather than by a substitution effected by the optic thalamus.

Images in space, orientation.—A portion of the fibres of the optic nerve, instead of proceeding to the cortex and the optic thalamus, follows the superior cerebellar peduncle (from before backwards) and passes to the cerebellum. This *direct cerebellar tract of retinal or optic* origin is the equivalent of the direct cerebellar tract of medullary or tactile origin, as well as of the direct cerebellar tract of vestibular origin, these two latter reaching the cerebellum by the inferior cerebellar peduncle. These three tracts cause the convergence towards the cerebellum of impulses originating in three different senses or apparatus (sight, touch, vestibular apparatus) which are in it organized into images of space with the aim of objective and subjective orientation (Bonnier). An indirect communication is established between the retina and the cerebellum by the intermediation of the olive, and the nuclei of the pons. The retina also sends fibres to the oculo-motor nuclei, either by the corpora quadrigemina or directly ; whence arises an apparatus of ocular adaptation simpler and still less conscious than the preceding one.

D. MOTOR EFFECTS—PATHS OF RETURN

Impulses have innumerable paths in order to descend from the cerebral cortex to the agents executive of movements ; but we shall here consider only those which are directly necessary or useful to the exercise of the functions of vision itself, and which form, with the so-called centripetal visual paths, a system whose component parts, being mutually connected by a functional bond of union, work in co-operation. It remains therefore to point out these paths and to analyse their mode of action.

We cannot too often repeat that all impulses coming from the external world do not penetrate the nervous system to the same depth ; some do not reach the cerebral cortex, and others do not approach it

to the same extent. Most of the halting places imposed upon the impulse by the grey matter in its journey (perhaps all of them) offer paths of reflexion to it, which are utilized or not according to circumstances. To ascertain with certainty what determines the variable progress of these impulses through such multiple and complex paths is one of the most important problems of physiology, but it is also one concerning which all positive information is wanting. All we can do is to connect it with a statement of a very general order which demonstrates, in the form of a classical formula, the function creating the organ. *The impulse in its progress obeys the same law as self-organizing matter. It goes where it is wanted.* Thus, just as in nervous phenomena which the simplifying tendencies of science permit us to willingly regard as a series of passive acts obeying an impulse from without, we are led to invoke a *clinamen*, not only original, but also incessant.

1. **Localities for reflexion of impulses.**—Whatever may be the conditions determining its course, the impulse is reflected, sometimes by the cortex and sometimes by the grey masses of the basal ganglia. The retina, the first locality reached by the nervous wave which arises at its surface, may perhaps present reflex microscopic arcs, whose smallness alone would prevent their submission to experimental investigation. This organ thus removed, there remain several others for us to examine from the same point of view. Like the sensory paths, the motor paths are complex and divided into different classes according to the order either of their juxtaposition or of their superposition, and the functional connexions attaching them to the preceding are very numerous. We can show this by only a few of the most characteristic examples.

Voluntary reflex and automatic movements.—Our eyes sometimes look for objects in the direction in which they are to be found by movements which we call voluntary, and they sometimes passively receive the luminous impulses from objects in front of them ; but even in the latter case the motor ocular apparatus is not independent of the visual act, with this difference, that the motor act then becomes instinctive or reflex. Hardly has the object to which our attention is drawn thrown its image on some portion of the retina, than the ocular muscles place the eye in an appropriate position for receiving this image on the area of distinct vision, if it is not already located there (line of fixation of the axis of vision). We may add that in ordinary vision, which is binocular, the movements of the two eyes are mutually coordinated for the formation of images on corresponding points of the retina. This example shows in how permanent a manner sensibility is solidarized with movement.

This dependence between sensation and movement and reciprocally exists in other cases besides that of fixation of the axis of vision. The axes of vision in each of the two eyes are not in reality parallel, but converge toward the object looked at, and the convergence progressively increases in proportion to the nearness of the object. The due regulation of these convergent movements is assured by a reflex association distinct from the preceding.

Movements as a whole; internal movements.—Besides these movements of the eyes as a whole, there are yet others in the interior of the eyeball which are equally necessary for the proper performance of the visual function. These are those which regulate the diameter of the diaphragm formed by the iris, and hence the illumination of the retina; and also the curvature of the crystalline lens for accommodation for near vision. Hence arise also other reflex systems, added to the preceding ones, for each of these acts taken individually.

All these acts are mutually co-ordinated in order to operate as a whole, but their dissociation is possible, and disease brings it about in different ways (Parinaud).

2. **Different functional associations.**—The movements of the ocular apparatus, and the associations of the nervous system governing and characterizing them, may thus be classed under four principal headings. All are to a certain extent of a reflex nature, whatever may be the degree of associated consciousness. These are :—

(1) *Associated movements of direction*, which maintain the parallelism (relative) between the ocular axes which is necessary for the due performance of binocular vision.

(2) *Associated movements of convergence*, which determine, between these axes, the value of the angle which causes them to cross on the object looked at, according to the distance at which it is situated.

These two varieties of movements are performed by the extrinsic muscles of the eye, and are to some extent regulated by associations which exist in the nuclei of the third and the sixth pair of cranial nerves. Their co-ordination with the movements, either of the head or of the body, in the varied acts in which they participate, necessitates the intervention of the cerebellum and of the brain, and, in the latter especially, the associations are different and have different seats according to the more or less conscious or voluntary nature of these movements. Even when the cerebral cortex participates in their production, these movements are not necessarily voluntary, but are frequently reflex or instinctive.

(3) *Movements of the pupil* regulating the quantity of light which enters the eye.

(4) *Alterations in the curvature of the crystalline lens*, which regulate the accommodation of the eye for distant vision. These two last-named are movements performed by muscles internal to the eye itself,

namely, the sphincter muscle of the iris and the ciliary muscle which increases the anterior curvature of the crystalline lens.

The two last species of movement are of an entirely unconscious and involuntary order. They are dependent upon the great sympathetic and its bulbo-medullary centres. As belonging to the great sympathetic must also be considered the elements contained in the oculo-motor nerve, which, leaving the latter, traverse the ophthalmic ganglion and form the ciliary nerves in connexion with the cervical spinal cord. These fibres, arising from a distinct portion of the nucleus of the third pair, form one only of the origins (the highest) of the sympathetic system. The localities of association and reflexion of impressions which control these movements are graduated in the corresponding ganglia of the sympathetic, in the grey bulbo-medullary axis, and in the grey masses surmounting it, especially in the anterior corpora quadrigemina.

These movements may be elicited both by the optic thalamus and the cerebral cortex. In emotional conditions the pupil is observed to dilate, and at the same time the eye tends to project, so as to protrude through the eyelids.

This last movement is due to a parallel influence (but one that is fundamentally distinct) of the great sympathetic on the smooth muscles of the capsule of Tenon, and on those which are contained in the thickness of the eyelids, perpendicular to the palpebral cleft.

The medulla oblongata through the ganglionic elements of the oculo-motor nucleus, and the cervico-thoracic spinal cord through the fibres of the cervical sympathetic which arise therein, represent two antagonistic influences acting on the movements of the pupil and on accommodation. The bulbar influence causes the sphincter iridis (pupillary contraction) and the ciliary muscle (convexity of the crystalline lens) to contract simultaneously; the medullary influences causes the pupil to dilate and the crystalline lens to become flattened—a double effect attributable either to the inhibition of the sphincter iridis and ciliary muscles, or to contraction of muscular layers where action is antagonistic, and whose existence seems to be demonstrated, at least so far as regards the pupil (Grynfeld). We may add that the bulbar influence is not univocal, since the trigeminal contains, even in its origins, a certain number of elements acting in the same manner as the cervical sympathetic, and which are hence connected with the sympathetic system as a whole. It thus follows that the pupillary mechanism and that of accommodation take their origin from a great extent of the grey bulbo-medullary axis, which conflicts with the hypothesis of the existence of a cilio-spinal centre located in a circumscribed point of the spinal cord. This separation of the pupillary nerves and those of accommodation into two groups is connected with the constitution of the great sympathetic, whose nuclei of origin are separated into distinct and discontinuous masses. For the purpose of mutual co-operation these nuclei are connected by bundles appertaining to the longitudinal bandalette, whose fibres thus perform the duties of elements of association.

Photo-mechanical reaction.—According to Engelmann, the action of light on the retina causes a contraction of the pigmentary cells and of the internal segments of the cones, which are, on the contrary, elongated in darkness. This contraction is rendered evident by the comparison of two isolated eyes of an animal (frog), one submitted to the action of light and the other kept in darkness. If the intact animal is operated on, by exposing one eye to the light while the other is covered up, the contraction occurs on both sides. If the skin of the animal is brilliantly illuminated while the eyes are in darkness, the result is the same. If, on the contrary, the brain be destroyed the photo-mechanical reaction at a distance no longer takes place. These facts seem to prove the existence of

a *reflex* whose centripetal and centrifugal paths are contained in the optic nerve, and whose centre is situated in some encephalic ganglion. Anatomy teaches us that centrifugal elements are not wanting in the optic nerve (see below, p. 597).

It needs only to be remarked that, up to the present, the terminal connexions of these centrifugal elements have not been ascertained to exist with the cones, but rather with the spongioblasts of the retina. However this may be, this photo-mechanical reaction should be considered as a reflex of *adaptation* of the nature of the photo-pupillary reaction, which also is transmitted from one eye to the other.

The cones, which have often been called nerve elements, are (like the pigmentary cells of the retina) epithelial elements differentiated to subserve the visual function. Like the cells of the skin, they are outside the nervous system, although in direct contact with it. Their contractile property, which may be compared with that of certain epithelia in no way prejudices that of being strictly nerve elements. The remarkable feature of this experiment is the fact of the initial stimulation (by luminous radiation) re-acting, after reflexion, on the same element (cone) which served it as a gate of entrance. But the mechanical movement in which it is here extinguished is not capable of causing this stimulation again to arise in the retina, at least in a conscious state. We have proof of this in the fact that the illumination of one eye, the other being closed, does not produce phosphenes in the latter.

3. **Retino-pupillary reflex.**—When a candle is brought near to the open eye, the pupil will be seen to shrink by the contraction of the iris; it once more dilates when the light is removed (it will always be found dilated if the eye be abruptly opened after being closed for some moments). This is a reflex act whose principal paths were traced by Herbert Mayo, and

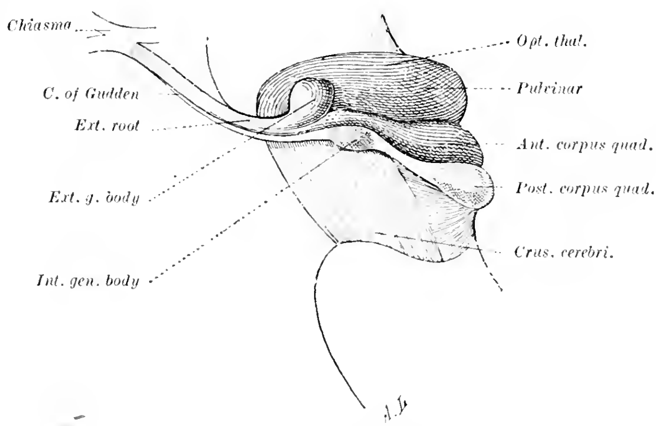


FIG. 234.—Optic tracts and ganglionic centres. Left lateral aspect (after Charpy).

especially by Longet. These authors observed that, if the optic nerve be cut, stimulation (pinching) of the ocular end is without effect on the pupil, while that of the encephalic end causes it to contract. This is the path of the inward journey. The contraction is not limited to the pupil of the corresponding eye, but is also observed in the opposite eye (Longet); thus there is passage of the impulse from one side to the other, as occurs in many reflex acts. The path of *return* lies in the fibres of the oculo-motor which are given

off from this trunk (thick and short ramification) in order to pass through the ophthalmic ganglion and to reach, by the ciliary nerves, the plexus which is situated at their termination in the iris. These are ganglionic motor nerves of the same nature as those forming the great sympathetic, with which it is convenient to connect them. The path of *reflexion* has been located by the preceding authors in the corpora quadrigemina (in mammals), or bigemina, still called optic lobes (in birds). Their opinion is possibly supported by certain clinical observations, although some authors consider that this reflex centre should be situated either in the grey matter of the third ventricle (Bechterew) or in the ganglion of the habenula (Mendel).

Visual and reflex fibres.—Thus the optic nerve transmits impulses, some of which go to the cortex to give rise in it to visual sensation ; others to the cerebellum, to assist orientation : and, lastly, others are reflected *en route*, so as to ensure their return to the iris. These impulses have not, perhaps, exactly the same starting point in the retina ; the first may be produced by shock of the cones, and the second by that of the rods. In any case, after leaving the optic nerve, they follow two orders of fibres, two different routes. The optic nerve, in the midst of finer fibres, which are the visual fibres, contains others (thicker) which proceed to the cerebellum and to the anterior corpus quadrigeminum, controlling by a reflex path the movements of orientation and of the pupil. Their respective attributes are rendered evident by the fact that lesions limited to the anterior corpus quadrigeminum leave vision intact and suppress the pupillary reflex (they also react on the movements of the eyes) (Monakow).

A lesion bearing upon the optic radiations, above the corpora quadrigemina, causes blindness, but allows of the persistence of the light reflex ; a lesion which occurs in front of the corpora quadrigemina abolishes at the same time both vision and the reflex.

Hemiopic pupillary reaction.—Should the lesion affect the optic tract on one side, it causes, as is well known, homonymous hemianopsia ; the two homonymous halves of the retinæ become insensitive to light, both from a visual and a reflex point of view ; the other two halves are sensitive, and, if illuminated, the sensation of light and the pupillary reflex are produced at the same time.

Reflex of accommodation and of convergence.—Reflex impulses gaining the pupillary muscle have more than one source and course ; these are numerous, as is shown by the following clinical fact.

Argyll-Robertson noticed in certain diseases, such as locomotor ataxia and general paralysis, that, although the light reflex had disappeared, the movements of the iris (also reflex) which are connected with accommodation and with similar movements causing convergence of the two eyes still persisted. These two reflex cycles which functionally produce the same motor result (contraction of the pupils) and which employ the same path of return (ciliary ramifications emanating from the oculo-motor), have therefore distinct paths and a different starting point.

4. **Associated movements.**—Thus we find that there is a reflex of direction, a reflex of convergence, a reflex of illumination, a reflex of accommodation, and to these may be added reflexes of protection, which we shall speak of later.

The starting-point of all these reflexes may be retinal stimulation,

and usually lies in this stimulation. If an object is in the field of vision and attracts attention, both eyes are very accurately fixed on it in order to receive its image on the yellow spot (reflex of direction); the two ocular axes converge exactly on the object, so that its image is thrown on identical points of the retina (reflex of convergence); the more or less intense light emanating from the object acts on the diameter of the pupil (reflex of illumination); the curvature of the crystalline lens is adjusted so as to give a distinct image on the retina (reflex of accommodation).

Far from being absolutely independent, each of these reflexes involves the others under certain circumstances. The reflex of convergence is connected with that of accommodation, and necessarily so, since the effort of convergence and accommodation is exerted in the same degree proportionably to the approach of the object. These two reflexes in their turn involve in a certain measure the pupillary reflex, and this is why in near vision the pupil undergoes a certain degree of contraction independently of illumination.

In the hallucinations of sight, changes of dimensions in the pupillary orifice may be observed, probably connected with efforts of accommodation instigated by changes of distance of imaginary objects (Ferré).

5. **Hemi-oculo-motor nerves; oculo-dextrogyral and oculo-levogyral nerves.**—As Grasset has observed, simultaneously with a *right hemiopic* nerve in connexion with the right halves of the retinæ, and a *left hemiopic* nerve which is connected with the left halves of the retinæ (these nerves being represented by the optic tract and the optic radiation on each side), there exists also in the brain on each side a *hemi-oculo-motor nerve*, which, being divided at the periphery between the two eyeballs, turns them simultaneously to the right (*dextrogyral* nerve), and also simultaneously to the left (*levogyral* nerve) (Grasset).

The dextrogyral nerve arises in the left hemisphere, and the levogyral nerve in the right hemisphere.—Experiment has proved this, for if an oculo-motor cortical area be stimulated on the left, the eyes turn to the right, and conversely when a right cortical area is stimulated. Clinical investigation also proves it, as after destruction of certain parts of the cortex, *a conjugated deviation of the eyes* has been observed, which results from the paralysis of one of the two hemi-oculo-motor nerves. If this destruction is seated on the right, the eyes are turned to the right; but if on the left they deviate to the left; this has given rise to the mnemotechnical formula: "the patient looks at his lesion." Paralysis of the motor area produces in fact a deviation the direct opposite of that produced by stimulation; this paralytic deviation is due to the persistence of an antagonistic motor influence.

Comparison with the sensory path.—We have seen above that when one of the lobes of the brain is destroyed as regards its visual area, the hemianopsia is homonymous; we have just said that in such a case hemi-oculo-motor paralysis when it occurs is on the contrary heteronymous, since the paralysed muscles are those which produce the movement to the right when the left hemisphere is injured, and reciprocally.

Comparison of the sensorial paths and the motor paths.—If the arrangement of the sensorial paths of vision be compared with that of the oculo-motor paths, a certain resemblance will be observed between them; but they are far from being interchangeable. In both we remark conducting tracts connecting each hemisphere of the brain, one to the two right portions, the other to the two left portions of each eyeball (retina in one case, muscles in the other). This distribution implies a crossing of at least a portion of the conducting fibres. This crossing as concerns the sensorial paths is a partial one, and takes place in the chiasma of the optic nerves. As regards the motor paths, it is at first complete, but becomes partial from the fact that the impulse in order to reach certain muscles (the internal recti) twice crosses the median line.

In fact, the dextrogyral cerebral nerve crosses the levogyral cerebral nerve in the mesencephalon to reach the motor nuclei of the eye. When leaving these nuclei a part of the fibres (those of the external motor nerve for the external rectus muscle) remaining on the same side, are direct; another part (those destined for the internal rectus), are crossed. In detail the arrangement differs according to whether, with Duval and Laborde, we consider that the fibres destined for the opposite internal rectus muscle start from the external motor nucleus of the same side, or with Spitzka that they take as a starting-point the nucleus of the oculo-motor also of the same side. In both cases they must decussate, and the impulse which has once surmounted the median line with the cerebral nerve, when destined for these fibres crosses them anew while following them.

Double crossing.—The successive double crossing of the paths of the impulse in the nervous system is not an exceptional fact; experiment shows that it even may be very frequent. An exceptional fact would be for the *same neuron* to undergo this double crossing in its length. An example of this is unknown, and in the case of the motor nerves of the eye, there is a stage of grey matter between the two inverse changes of direction given to the impulse.

Thus, the hemi-oculo-motor nerve conducts the impulses of one hemisphere to the muscles of the two halves of the eyeball opposed to its own situations (left for right, and reciprocally) and turns the eyes in this direction opposite to its own. The hemiopic nerve conducts to one of the hemispheres the impressions of the two half retinæ situated on the same side as itself (right for right, left for left), but the reversal of the situation of the images and of the images themselves in connexion with the objects being granted, each hemisphere sees the objects placed on the side opposite to itself. This remark holds good for the yellow spot as well as for the peri-macular area of the retina, since the macular tract acts in the same way alone as does the optic nerve as a whole.

Distinct vision only being possible in the yellow spot, the ocular axes are directed instinctively to the centre of the objects looked at, so that their image is thrown on the yellow spot: this is the reflex of direction. This reflex of direction has for starting-point, when the object is situated laterally, a visual impression which is made on the halves of the retinæ opposite to the object (reversal of the situation of the images): this impression is conducted to the hemisphere homonymous to these half retinæ, and, like them, opposed to the object. In this hemisphere it finds conditions of reflexion and motor paths which bring it back to the muscles, whose contraction places the yellow spot opposite the object, that is to say, in the prolongation of a straight line which passes through the centre of the eye and the object.

6. **The elevator and depressor nerves of the axis of vision.** — The existence of two hemi-oculo-motor nerves, the one dextrogyral and the other levogyral, leads us to suspect the parallel existence of an *elevator* and a *depressor* nerve of the axis of vision. The dextro- and levogyral nerves are rendered anatomically visible and independent by the existence of the interhemispherical fissure which separates the brain into two right and left halves in relation to the median plane. But nothing of the kind is found which would suggest the existence of two nerves, one of which acts as an elevator and the other as a depressor of the axis of vision. The fibres of both are necessarily distributed in the axis of vision. The component fibres of both are necessarily distributed in the two halves of the brain. The two halves of both are solidarized in their functions by connexions which probably exist either in the two hemispheres through the commissures (corpus callosum), or in the mesencephalon at the strengthening point between the cerebral and peripheral neurons. These two halves are on the other hand functionally independent, to allow of their isolated antagonistic action.

7. **Movements of the eye in their relations with the muscles and the peripheral motor nerves.**—All movements of the eyes except those in a transverse direction require associations, both nervous and muscular, which are rather more complicated than those of these latter; this fact stands out markedly from an analysis of the movements of one eye considered independently.

The movements of the eye are all movements of rotation round a point coinciding with the centre of the organ regarded as forming a sphere. We will examine those which are carried out round the three different principal axes; the *antero-posterior* axis (movement of rotation of the pupil on itself); the *transverse* axis (movements of elevation and depression). and the *vertical* axis (movements of abduction and adduction of the pupil). Three pairs of muscles (the four recti and the two obliqui) ensure the performance of these movements. If each of these pairs of muscles (inferior and superior recti, internal and external recti, superior and inferior obliqui) were individually situated in a plane exactly perpendicular to each of these axes, the conditions of their intervention for the production of the before-mentioned movements (cardinal movements) would be simple, and from this fact very distinct. But in reality only the external rectus and the internal rectus are in this condition. All the other muscles, including the inferior and superior recti (which, in fact, are oblique), form a more or less open angle with the direction of the above-mentioned planes. Therefore it becomes necessary that the position of the eye that one of them produces by contracting alone should be

corrected by the contraction of one of the obliqui whose obliquity is in a contrary direction to its own. It is for this that the inferior oblique is associated with the superior rectus to raise the pupil, and the superior oblique with the inferior rectus to lower it.

For the performance of diagonal movements, that is to say, of those which place the eye in positions intermediate between the four cardinal positions above described, the help of three and not of two muscles is required, as may be rendered evident by pictures or diagrams.

Antagonism in repose.—The obliqui muscles (superior and inferior) are, practically, in a certain degree antagonistic to the recti (superior and inferior). They are so not only in a state of contraction, properly so called, for the execution of the movements of the eye, but also in the tonic condition necessary for maintaining the eye in the orbital cavity. In fact, the four recti by their simultaneous contraction, whether tonic or otherwise, tend to sink the eyeball in the orbit; the obliqui, by reason of their situation and the direction of their insertions, exert an opposite tendency; they support the eye posteriorly like a girdle, and tend to restrain it in front. Other muscular elements are contained in the ocular leaflet of the orbital aponeurosis.

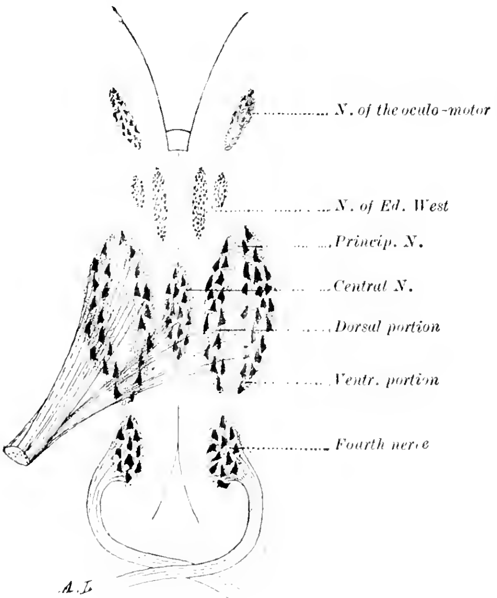


FIG. 235.—Nuclei of the oculo-motor nerve. Diagram showing their anatomical arrangement (Charpy).

Individual centres for the muscles of the eye.—If from the muscles we now pass to the study of the nerves directly controlling them, we may consider that each muscle of the eye is, as it were, provided with a special nerve, by maintaining, what is indeed true, that each of the branches of the oculo-motor nerve proceeds from a special centre forming a portion of the total centre of this nerve. Each of these nerves may act independently of all the other nerves of the same side, but not independently of those of the opposite side. The twelve motor nerves of the eye, or rather their twelve centres, are connected either in twos, or in a larger number, between the two sides, independently

of the associations which they mutually form on the same side for the performance of the different movements considered above. It will be at once obvious that, in these associated movements of the two eyes, the lateral movements must be distinguished from those of elevation and depression of the eyeballs. These latter movements are, in fact, *symmetrical* in the ordinary sense of the word. The first-named cannot be so, inasmuch as a movement of adduction of the eyeball on one side must correspond with a movement of abduction of the ocular globe on the other side. To explain the correlated action of the external oculo-motor nerve of one side with the internal branch of the oculo-motor nerve of the other side, it is held that this branch, merely attached to the oculo-motor nerve, arises in reality, by decussation and crossing of its fibres on the median line of the bulb from the same centre as that of the external oculo-motor of the opposite side. Pathological facts support this manner of viewing the question. The same reasoning holds good as regards the branch of the oculo-motor which supplies the inferior oblique: it should arise from the centre of the fourth nerve of the opposite side.

Principal directions of the movements of the ball of the eye, in their relation with the muscles executing them.

Cardinal movements.	Intermediate movements.	Participating muscles.
Adduction	..	*Internal rectus*
..	Adduction and elevation	*Internal rectus* *Superior rectus* *Inferior oblique.*
Elevation	..	*Superior rectus.* *Inferior oblique.*
..	Abduction and elevation.	*External rectus.* *Superior rectus.* *Inferior oblique.*
Abduction	..	*External rectus.*
..	Abduction and lowering.	*External rectus.* *Inferior rectus.* *Superior oblique.*
Lowering	..	*Inferior rectus.* *Superior oblique.*
..	Adduction and lowering.	*Internal rectus.* *Inferior rectus.* *Superior oblique.*

Some authors have maintained that, when the head is inclined toward one or the other shoulder, the two eyeballs perform a rotatory movement in the orbit which is corrective of the preceding one. By the help of very exact data, it has been demonstrated that this compensatory movement does not occur: it is not possible for the eye to move on its antero-posterior axis (Contejean).

8. **Inhibitory paths.**—Thus from the cortex (in the frontal and occipital areas) the impulses may descend through certain fibres of the corona radiata and of the internal capsule to the motor nuclei of the muscles of the eye in order to elicit movements of these muscles. These exclusively motor fibres have, nevertheless, different functions, inasmuch as, according to which of them is stimulated, the eyeballs will assume different positions, turning either upwards or downwards, to right or to left, or else assuming the intermediate positions. From the manner in which they distribute the impulse to the bulbar nuclei of the oculo-motor nerves, and also from the way in which they associate the six partial groups of the fibres of these nerves (the six nerves which proceed to the six muscles of the eye) they give rise to co-ordinated movements of the eyeballs which are in relation with their special function. Like the motor areas from which they arise, they represent these movements, since it is sufficient to arouse their activity, even by artificial stimulation, for the whole series of the acts producing them to be brought into being.

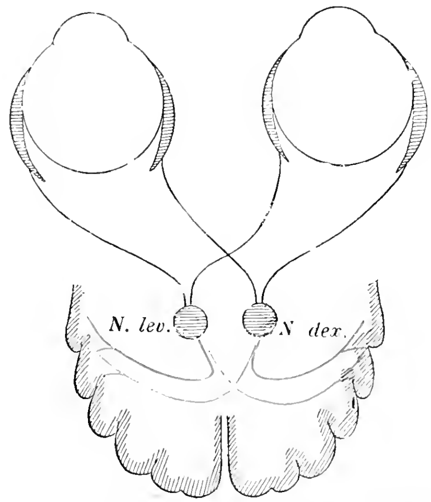


FIG. 236.—Hemioculo-motor nerves.

Bulbo-muscular neurons in black; cortico-bulbar neurons coloured.

These latter neurons are of two orders, some excito-motor as regards the bulbar nuclei (in blue); the others inhibitory as concerns these nuclei (in red).

The simultaneous action of the cortico-bulbar neurons of one of the two hemispheres has the effect of stimulating the nucleus of one side, and inhibiting that of the other.

Therefore there must be a double motor cortical area to ensure the arrival at the ocular muscles of impulses of various nature and origin; some, sensorial, coming from the retina, others, sensory, coming from the sensitive portions of the eye, or also from other parts of the sensory field and from other senses; there must also be in each of these areas functionally differentiated fibres for the realization of the different co-ordinated movements of the eyeballs. This multiplicity of functions, each requiring a co-ordinated system for its performance, explains the very extended development of the cerebral cortex, and also the large number of fibres of projection uniting it to the grey bulbar or supra-bulbar masses, whence arise the nerves which directly supply the muscles. But the complication of these systems does not stop here.

Alongside of these excito-motor fibres are others possessing an inhibitory function. These elements, whose existence in the brain had long been suspected, have been demonstrated by Sherrington as regards the oculo-motor functions by the aid of interesting experiments. Here are the facts.

Experiment.—In one of the cerebral hemispheres (say the left) in a dog one of the motor areas (frontal or occipital) is laid bare and stimulated ; the stimulation of this area will cause deviation of both eyes to the right (it must not be forgotten that the dextrogyral nerve starts from the left hemisphere, and the levogyral nerve from the right hemisphere).

This deviation is usually attributed to an excito-motor action which, leaving the cortex, reaches in a parallel and simultaneous manner the internal rectus muscle of the left eye and the external rectus muscle of the right eye by the motor branches for these muscles, namely : the internal branch of the left oculo-motor nerve and the right external oculo-motor nerve of the right eye. Having verified this, the left oculo-motor and the left pathetic nerves are cut, that is to say, all the motor nerves of the eyeball with the exception of the external oculo-motor supplying the external rectus. This section (especially that of the oculo-motor) is performed with the aim in view of closing to the impulse all paths going to the internal rectus muscle of the left eye ; the muscles thus deprived of their nerve supply must be left intact, so that their elastic tension may prevent the eye from being completely deviated outwards, towards the temporal boundary of the orbit.

The same stimulation is again applied to the same area of the cortex. The result is once more a conjugated movement of both eyes to the right. The right eye turns rapidly, the left eye slowly, but both deviate in the same direction, that is to say, to the right, as before. How can we explain this deviation of the left eye to the right, when the internal rectus of this eye has lost all connexion with the brain, and even with the medulla oblongata, and when the only connexion remaining between the brain, the bulb and the left eye is represented by a nerve, the external oculo-motor, supplying a muscle, the external rectus, whose contraction produces an exactly opposite movement ? The only admissible explanation is that the impulse which, from the brain, proceeds to this muscle, has weakened the tone of the latter. This tonic contraction of the external rectus muscle which overcame the elasticity of the enervated internal rectus muscle and thus caused the left eye to turn slightly outwards, having ceased, this eye undergoes a relative movement of rotation towards the right, a movement which is itself limited by the elasticity of the external rectus muscle. *The deviation of the left eye towards the right does not in this case result from the activity of its internal rectus muscle, but from the lessened resistance of its external rectus muscle, this being the only one, under the conditions of the experiment, capable of being influenced by the stimulation.*

Inhibition by stimulation of the white matter.—This inhibitory effect is obtained not only by stimulation of the cortex, but also, after removal of the latter, by stimulation of the corona radiata, both in the frontal and occipital region ; or by that of the internal capsule, when applied to two points situated behind the knee ; or, lastly, by that of a section of the corpus callosum, 3 to 5 millimetres behind the knee, or in the region of the splenium.

Locality of inhibition.—The locality in which the inhibitory phenomenon is manifested is not then the cerebral cortex, whose presence,

as we have seen, is in no way necessary. Where, then, is this locality situated? It is not located in the spot where stimulation is brought to bear; that is to say, at the origin of the stimulated fibre, neither is it in the ultimate termination of the motor system, namely, the muscle. *It is situated in the grey supra-bulbar nuclei at the point of union between the fibres of the corona radiata and the oculo-motor nerves.* It is the tonic activity of these grey nuclei which is weakened by the intervention of the cerebral inhibitory fibres. The inhibition is effected by one nerve fibre on another, and not by a nerve fibre on a muscle; but no decisive proof can be brought forward.[1]

The direct stimulation of the external oculo-motor, like that of the other motor nerves of the eye, or, more generally, of any nerve proceeding to a muscle without interposition of grey matter, has only one effect which is invariably the same: the contraction of the muscle and never its relaxation. For the production of an inhibitory influence the interposition of a nucleus of grey matter between the segment of nerve stimulated and the muscle under consideration is required, that is to say, according to the definition given of "grey matter," the interposition of a locality in which, between the terminal and initial extremities of the neurons uniting this grey matter, that special conflict from which arises the suspension of motor activity characterizing inhibition may be effected.

Another example.—Sherrington has added to the variations of his important experiment. The oculo-motor and the pathetic nerves are cut on the right and left, while the external oculo-motor nerves of the two sides are left intact. A certain degree of divergent strabismus ensues by the predominant action of the two nerves left unimpaired. Then the two oculo-motor areas of the right and left hemispheres are simultaneously stimulated: the two eyeballs are brought back to their primary position, with a certain degree of convergence. The same reason and the same explanation apply as given above. The double stimulation thus brought to bear has not been able to restore the enfeebled activity of the internal recti, but it has momentarily suspended that of the grey nuclei governing the external recti, and the effect has been the same. When two antagonistic forces are contending for the production of a movement, the direction of the latter may be determined, either by increasing one force (which is called in neurology *motor effect*), or by diminishing the other (*inhibitory effect*).

Comparison.—Generalization.—This experiment may be compared with a former one, which is altogether analogous, performed on the great sympathetic (in the rabbit). Stimulation of the cervical segment of this nerve causes contraction of the vessels of the ear, as is well known from the experiments of Cl. Bernard and of Brown-Séquard. Stimulation of the superior portion of the thoracic segment causes relaxation of these vessels (Dastre and Morat).

It may also happen that this latter stimulation may cause them to contract.

[1] When the inhibitory action seems to be exerted at the termination of the nerve in the muscle, as in the case of the pneumogastric with regard to the heart, it is easy to show that between the nervous termination and the muscular fibre, grey matter is interposed under the form of ganglia or of a ganglionic plexus, this being a confirmation of the formula of inhibition as stated here.

The thoracic chain is in fact (as regards the vessels of the ear) a mixture of elements, some excito-motor, and others inhibitory ; as a rule the latter predominate in it. The area of grey matter (in every case according to the definition given of the latter) in which the conflict between one and the other occurs, is located in the sympathetic ganglia of the base of the neck (first thoracic and inferior cervical ganglia). These two examples, one taken from the great sympathetic, the other from the encephalon, uphold the general conception which may be held of the mechanism of inhibition, and which similar experiments have extended to the invertebrata (Physalix).

Part taken by inhibition in the conjugated deviation of the eyes.—To explain how the activity of a single cerebral hemisphere causes both eyes to deviate in a manner which is neither convergent nor divergent, but mutually parallel either to right or to left, it has been suggested that each hemisphere possesses a *cortico-bulbar* nerve which, after being reinforced in the bulbar nuclei, is prolonged outwards by two branches, one *direct,* going to the muscle on the same side, and the other *crossed,* proceeding to the muscle on the opposite side.

Theoretically, this explanation appears sufficient so far as regards the conjugated movements of the eyes, and also of their persistent deviation in certain cerebral affections ; but experiment, having demonstrated the existence of inhibitory fibres added to the preceding, they must be taken into account, and a suitable position must be found for them in the explanatory scheme. The function of these inhibitory fibres cannot be simply and entirely to oppose the preceding, thus squandering and wasting the exciting and directing energy of the nervous system ; rather is their function that of economizing this energy, with the aim of facilitating and perfecting its activity.

The most general law appears to be the following one : *when two muscles contend for the performance of a movement, once the direction of this movement is determined, a correlated action is initiated between the inhibitory fibres of the one and the excito-motor fibres of the other.* That is to say, two nervous actions are produced in a parallel and simultaneous manner, one to augment the exciting energy of the muscle which is to commence acting, and the other to diminish the exciting energy of the opposed muscle, and therefore its resistance. This at least is what would happen in ordinary functions, and what we should observe in the cases which are most amenable to experiment. Oculo-motor innervation is a case of this kind.

By analogy with the teaching of experiment, in the lateral conjugated movements of the eyes we may admit that inhibition intervenes in the elevation and the depression of the axis of vision ; the exciting influence of the cerebral elevator nerve on the motor nuclei which raise the eye must be complicated by an inhibitory influence of this nerve on the motor antagonistic apparatus which tends to prevent its rise or to depress it.

Inhibitory and motor elements.—The question as to whether the inhibitory are distinct from the motor fibres, or whether the same elements perform, in turn, both functions, has often been matter of discussion. In principle, experiment and logic agree in favouring the existence of a distinction between the two orders of fibres ; but the alternative is not so precise as may appear at first sight. If it be remembered that the phenomenon of inhibition is consummated at the terminal extremity of the stimulated fibre, and not at its initial extremity in the locality where the stimulation is received ; and if it be taken into consideration that this fibre, at its termination, is divided into *distinct branches,* it will be obvious that the impulse which it distributes in these branches may have in one of them a stimulating effect, and in another an inhibitory influence, according to the definite relations contracted by each of them with the succeeding nerve

elements. The motor or inhibitory specificity would belong to the branches of the neuron, and not to the neuron itself. This may apply to ocular inhibition in the experiment of Sherrington: a fibre of the corona radiata bifurcating in order to proceed to the nuclei of the external oculo-motor nerve of the two sides might, by one of its branches (that going to the nucleus of the opposite side) exert a motor influence, and by the other (the one going to the nucleus of the same side) play an inhibitory part. Specifically there is nothing to prevent this being so, because the two branches, one motor and the other inhibitory, are destined to constantly work in the performance (by opposite means) of strictly equal movements, although these movements may take place in separate organs (right and left eyes).

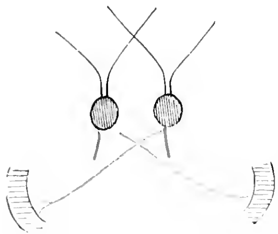


FIG. 237.—Cortico-bulbar neurons.

Their action is at the same time excito-motor as regards the active nucleus and inhibitory as concerns the opposite nucleus whose function is antagonistic.

In the case of strictly associated movements, like those of vision, it is sufficient for a single neuron leaving the cortex to have, by one of its terminations, an excito-motor action on one of the nuclei, and by another termination an inhibitory action on the antagonistic nucleus.

For unsymmetrical organs, like the heart, there is no necessity for such an arrangement.

9. **Other co-ordinated movements of the eyes.**—The lateral movements have an importance which may almost be considered as preponderating, and when the cortex is stimulated, they are the movements by which this stimulation is most readily rendered evident. To demonstrate the other movements of the eyeball, it is better to eliminate beforehand the influences giving rise to lateral movements. With this end in view, and if, for example, the left hemisphere is to be stimulated, the internal rectus of the left eye and the external rectus of the right eye should be cut. The stimulation will then, according to the point excited, give rise to upward and downward movements of the eyeball; or, again, to movements in the different quadrants; or, finally, to those of convergence (J. S. R. Russell).

It will thus be obvious that, in the brain, motor elements for all the co-ordinated movements of the eyes are present, these having as their object either movements of the axis of vision in all directions, or those of convergence of both eyes on objects which are more or less remote. To simplify the classification, we may distinguish between a *dextrogyral* nerve, a *levogyral* nerve, an *elevator* nerve and a *depressor* nerve of the axis of vision, without taking into account the intermediate movements resulting from their combinations; and, finally, a *nerve of convergence*, or at least of the association, which all these different movements and positions bring into being.

10. **Movements of the eyelids.**—The membranous veils which are lowered before the eyes to cover them in sleep, to uncover them in waking, and to protect and wash them in winking, are themselves con-

trolled by antagonistic muscles and nerves, whose balanced or predominating action determines their position on the eyeballs.

These muscles are the orbicularis palpebrarum, and the levator palpebræ superioris. The first is supplied by a branch of the facial (closure of the eyelids), the second by a branch of the oculo-motor (opening of the eyelids). These two small branches, belonging to complex nerves, enter into an antagonistic system which has some analogy with those of the preceding movements.

Here, again, we find numerous functional associations of the different nerves and muscles of the periphery, and multiplied utilizations of each of these motor peripheral apparatus according to the functions to be performed. When we look upwards, the upper eyelid is raised so as to uncover the eye and the two movements are strictly correlated, although at the same time independent. It is necessary for the will to interfere in a special manner in order to close the upper lids over eyes which are voluntarily raised. The branch and the motor centre of the levator palpebræ superioris are thus associated with the centres of the superior recti and the inferior oblique muscles for the performance of the action imposed on them by the nerve which is the elevator of the axis of vision.

Protective reflex.—The movements of the eyelids are connected with voluntary acts as regards the direction of the axis of vision, with emotional acts in the expression of certain sentiments, but are purely reflex in winking, which aims at the protection of the eye. The pupillary reflex is in numerous instances (but not always) a defensive reflex of nearly the same kind. If we enter into the detail of these actions we shall discover a large number of reflexes of the same nature, having their ultimate expression in acts which are not only motor, but also secretory, or, as is sometimes incorrectly stated, trophic. The blood supply of the eye, and especially of the retina, is also regulated by a reflex mechanism. Again, the eye is protected and preserved by secretions both of an external nature, as the secretion of *tears*, and also internal, like that maintaining the tone or ocular tension at its normal level. The nervous agents which regulate these vascular and secretory actions are located in the trigeminal and the great sympathetic, or, rather, in the sympathetic system whose origins are furnished by the trigeminal.

11.—**Movements of the head.**—When vision is directed to an object, Movements of the head are often associated with those of the eyes in order to bring them to bear in the desired direction ; the most obvious of these are the lateral movements. Experiments have pointed out the existence in the motor region of the cortex (and especially in the

frontal region) of an area for rotatory movements of the head in the vicinity of that for movements of the eyes. In the corona radiata there is a dextrogyral and also a *levogyral nerve of the head,* just as there is one of the eyes, and which is placed in its immediate neighbourhood. It has been demonstrated clinically that, in certain lesions of the cortex, deviation of the head accompanies that of the eyes and takes place in a similar direction.

These nerves belong to two categories, thus resembling the muscles whose movements they inspire. These two dextrogyral and levogyral nerves of the head are totally crossed (like those of the eyes), before reaching the motor nuclei of the nerves of the head in the mesocephalon (Grasset).

Some (posterior branches of the two first, and anterior branches of the four first cervical pairs) proceed to a group of rotatory muscles of the head of the same side, namely: splenius, large and small, rectus capitis posticus, and the obliquus capitis superior. Others (external branch of the spinal) proceed to a group of rotatory muscles of the opposite side: the sterno-mastoid and trapezius. The first proceed to their groups of muscles without decussation; the second, in order to act in correlation with them, must cross each other (in the same way as the fibres of the oculo-motor proceeding to the internal rectus muscle of the eye).

12. **Numerous motor areas for the eye.**—The data furnished by experiment in proportion as they become more numerous, show the fallacy of the far too simple conception which was at first held with regard to the localization of the sensory and motor functions in the brain. Contrary to what was originally maintained, *there is not merely one excitable motor area in the brain, but several such exist.* In fact, in addition to the Rolandic area, in which the movements of the limbs and face are represented, the existence of another has been ascertained; this last being situated in the area of the visual sphere controlling the muscles of the eyes; and a third will be found in the auditory sphere which governs the muscles of the ear. Nevertheless, these data are capable of reconciliation with the theory of cerebral localizations, but on the condition that it be expressed by a formula different from the one formerly made use of. Instead of dissociating and separating sensibility and motricity, they should, on the contrary, be strictly associated in the execution of different functions, and, after these have been distinguished from each other according to their most obvious characteristics, an effort should be made to discover if they are represented in any special area of the brain. In other words, localization must be brought to bear, not on the two modalities essential and necessary to the performance of the functions, but on these functions themselves.

This new theory having been formulated, we shall still find a difficulty in accepting it, as even though we may admit the correctness of the principle, it is not always easy to decide about its application.

Motor occipital area.—In the occipital lobe, *an ocular motor area exists which is more or less interchangeable with the visual sensory area,* and this agrees with the idea we hold concerning the nature, essentially reflex, of nervous functions; but in the frontal lobe, and therefore at some distance from the visual area, is another motor area for the eyes, one somewhat distinctly defined, and even more easily experimentally excitable than the preceding, and which must be taken into account in the cerebral topography. If surprise is caused by the sight of a double motor source converging in the cortex towards the same inferior centres and the same muscles, it must be remembered that the same peripheral apparatus is often used for very different functions. And if it be asked to what reflex arc these oculo-motor elements which duplicate those coming from the occipital lobe belong, we may answer that the ocular globe, over and above the special sensibility which has devolved on the retina, forms a portion of the field of general sensibility, notably through the cornea and the conjunctiva, these being very sensitive surfaces. No doubt the vicinity of these frontal oculo-motor areas with the tactile area of the Rolandic region is explained by a connexion between general sensibility and movement.

Independence of the frontal and occipital areas.—Have both motor areas their fibres of projection in the corona radiata, or does the stimulation of one of the two simply follow the fibres of association to reach the other, and to descend by a single path into the mesencephalic nuclei? The first of these suppositions is the true one. To demonstrate it the two areas must be stimulated after they have been separated by deep sections which interrupt the continuity of the fibres of association, or after the removal either of the frontal, or the temporal lobe; in both cases stimulation of one or the other will be followed by motor effects. Further, it has been observed that the excitability of the occipital area in young animals precedes by several days the appearance of that of the frontal area. They must then be quite distinct, and each corresponding to a system complete in itself is capable of operating in an independent manner.

Ophthalmoplegia.—If it be true, as some have maintained, that the visual area of the occipital lobe is blended with an oculo-motor area, destruction of the first must involve that of the second. Nevertheless, simple hemianopsia after the destruction of the cuneus, is not followed by a conjugated deviation of the eyes. It must be remarked with regard to this, that paralyses following destruction of limited areas of the cortex do not betray themselves by a total or even very evident loss of movement in muscles connected with the destroyed area. The

resulting functional deficiency takes effect only on special modalities of the movement, allowing the persistence of a somewhat large number of others; this explains the apparent integrity of the corresponding motricity. The destruction of the two visual areas, like that of the optic nerve itself, is only revealed by a change in the appearance of the eyes and a vagueness in the glance, due to a defect of convergence, and also to the situation of the eyelids. These organs have nevertheless retained all their mobility, and move under the influence of impressions of a reflex nature, or of those furnished them by other regions of the brain and the cortex, this latter being connected with other senses and functions besides that of vision properly so called.

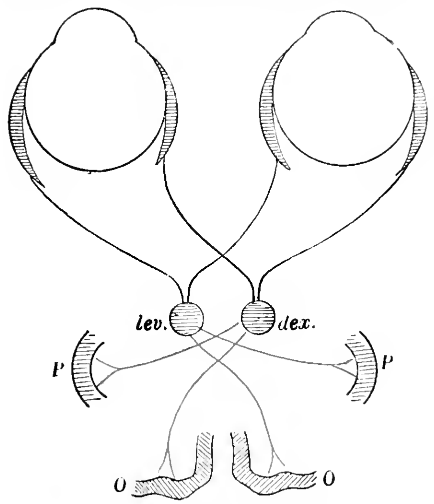


FIG. 238.—Hemioculo-motor nerves and centres.

Cortico-bulbar neurons in blue; bulbo-muscular in black.

dex, dextrogyral oculo-motor nucleus; *lev*, levogyral oculo-motor nucleus; PP, fronto-parietal cortex (tactile area) OO′, occipital cortex (visual area). The tactile and visual senses make use of, by independent nerves, the same oculo-motor nuclei for different functions.

A conjugated deviation of the eyes has been observed consecutive to lesions of certain portions of the cortex outside the visual area, using the word in its strict sense. Grasset and Landouzy have observed this deviation in the case of focal lesion of the parietal lobule at the angular gyrus (Grasset), near the foot of the ascending parietal (Landouzy). Ferrier has produced this deviation by stimulating the angular gyrus in the monkey. Munck has observed a disturbance of the ocular motility and also of the general sensibility of the eye to be the result of the extirpation of the inferior parietal lobule. When this region is artificially stimulated, as in Jacksonian epilepsy, the deviation is naturally in the opposite direction.

Grasset and Landouzy consider that the cerebral nerve, which is the elevator of the upper eyelid, also starts from the inferior parietal lobule, the destruction of this lobe being sometimes accompanied with blepharoptosis of the side opposed to the lesion. From the same region of the cortex the cerebral nerve which governs the antagonistic movement of closure of the eyelids (opposite side) is also considered to arise; this nerve corresponds to what is called the superior facial in opposition to the inferior facial supplying the muscles of the inferior portion of the face, whose cortical area is situated in the Rolandic region. Exner and Paneth, by stimulating the angular gyrus, have produced contractions of the orbicularis of the opposite side.

This dissociation, both anatomical and functional, of the two parts of the facial, one of which is destined for the orbicularis palpebrarum, and the other for the muscles properly so called, of the face, explains the fact often noticed in ordinary hemiplegia of the superior facial being immune or, at any rate, less markedly affected than the inferior facial.

At the same time, it must be noticed that blepharoptosis may also occur in ordinary hemiplegia as the result of lesion of the central convolutions, as the facial also possesses a source of innervation situated in these convolutions.

Paralysis of the orbicularis may also exclusively attack the voluntary move-

ments while ordinary reflexes and the power of closing the eyes during sleep are preserved. In other cases the purely reflex movements are the only ones retained. The reflex of occlusion produced in sleep has probably another locality of reflexion than the basal ganglia, possibly the cortex (Tournier).

Remarks.—Under the name of ophthalmoplegia are clinically indicated all paralyses of the extrinsic or intrinsic ocular movements, whether the cause be peripheral or central. It seems a pity that the word "ophthalmoplegia" has not been reserved to designate the ocular monoplegias of central origin, as have been the words "hemiplegia, paraplegia" to describe those paralyses of the other organs whose origin is in the spinal cord or the brain.

Dissociation of the occipital motor area.—Schaffer (1888), operating on the monkey, has demonstrated that stimulation of the internal surface of the occipital lobe in its medium region, produces lateral conjugated deviation of the eyes; stimulation applied to the superior portion of the occipital lobe causes the eyes to look downwards, and to the inferior portion upwards. (Bechterew has noticed analogous facts resulting from stimulating of the anterior and posterior portions of the same lobe; only the eyes, instead of occupying analogous or inverse positions, were deviated towards the quadrants.) Also movements of the eyelids and modification of the pupil may be obtained. These partial localizations, apparently so regular, of the oculo-motor cortical elements, cannot fail to exercise an effect on the minds of those who maintain the idea of a sort of geometrical projection of the retina on the visual area of the occipital lobe. Each of the cardinal points of the retina would be united functionally to the muscle (or muscular group) which causes the eye to deviate towards the four cardinal positions. This bond of union would be effected by a kind of cortical reflex of direction, the luminous impulses which fall in the first instance on each of these cardinal points having the effect of initiating the movement of the corresponding muscle in such a way as to place the eye in the position best adapted for distinct vision. Stimulation applied to the cortex would thus reach in an isolated manner each of these reflexes, and by bringing its motor portion into play thus demonstrate their respective situation. This reasoning may perhaps be exact, but we cannot help noticing a want of condensation about it and also how much it stands in need of support from new data.

13. **Influence of the cerebellum.**—Saucerotte, in the last century, suspected that the movements of the eyes were influenced by the cerebellum. Magendie has observed that if either the cerebellar peduncle or the pons varolii be cut the eyes are deviated downwards on the corresponding side, and upwards on the opposite side to the lesion. Destructions and stimulations of the cerebellum itself also modify the position and the movements of the eyes. The ablation of a cerebellar

lobe induces an alteration of such a nature that the eye of the side corresponding to the lesion looks downwards and inwards, sometimes nystagmus occurs (the head, the movements of which agree with those of the eyes, is inclined towards the lesion ; it is twisted around its axis, so that the muzzle seems to look at the healthy side and the occiput at the side operated on). In destruction of the vermis the eyeballs are the seat of a vertical nystagmus (the head is strongly inclined backward, the trunk curved in the same direction with opisthotonos, and the anterior limbs are forcibly extended) (Thomas).

Destruction and stimulation of the different portions of the cerebellum.—Localized excitation of the different lobes or portions of lobes on the surface of the cerebellum produces principally movements of the eyes. In stimulation of the lateral lobe both eyes look towards the stimulated lobe and at the same time upwards. Stimulation of the flocculus causes rotation of the eyes on their antero-posterior axes. In stimulation of the vermis in its anterior portion, the eyes look directly upwards, but in that of its posterior portion they are directed downwards ; it being always understood that the excitation is applied exactly on the median line, for should it be displaced laterally the action of looking upwards and below is complicated by a displacement of the same side, and these combined effects will produce a diagonal position. In stimulation of the pyramid of the median lobe, the eyes will move in a horizontal plane, directly to the right should the stimulation be applied on the right, directly to the left if it is applied on the left (Ferrier).

Whatever be the anatomical relationship between the cerebellar cortex and the motor nuclei of the eyes, experiment thus demonstrates in a very obvious manner the existence of an exciting and directing influence of the cerebellum on these nuclei and through them on the position of the axis of vision. This influence takes part in its turn by the help of afferent impulses conveyed to the cerebellum by centripetal paths. The sources of these stimulations are also numerous.

A portion of them come from the retina (direct cerebellar tract of the optic nerve), then from the tactile organs, and especially from those of the eyeball which are irritated by their changes of position ; lastly, and especially, from the semi-circular canals.

Destruction and stimulation of the semi-circular canals.—The internal ear possesses by means of its vestibular apparatus a very direct relation with the co-ordination of movements, those of the eyeball being comprised in it, this relation being distinctly demonstrated by experiments. The destruction of the labyrinth is accompanied by nystagmus and ocular deviation. This deviation much resembles that following the

ablation of a cerebellar lobe (deviation downwards with inclination of the head) (Thomas). Stimulation of the circular canals in the rabbit provokes movement of the eyes (Cyon). The direction of the movement varies according to the canal stimulated ; stimulation of the horizontal canal produces a rotation of the eye of the same side which turns it upwards and downwards : that of the transverse canal backwards and upwards, and that of the sagittal canal backwards and downwards ; in the opposite eye the movements are feebler and made in a contrary direction. Ewald has also found that stimulation of the labyrinth produced, it is true, by a different procedure, acts on the movements of the eyes ; only the direction it assumes differs from the preceding.

The relation between the optic nerve and the orientation of the axis of vision seems especially of a conscious nature and its mechanism appears to be principally cerebral. That between the labyrinthine apparatus and the movement of the eyes seems rather automatic, and of mesencephalic and cerebellar mechanism.

Centrifugal fibres in the optic nerve.—The optic nerve seems at the first glance to be composed exclusively of centripetal fibres devoted to the conduction of impressions received by the retina for transmission to the brain. It is in reality a mixed column, which contains centrifugal fibres though in a small proportion. This somewhat unexpected result, being very firmly established, deserves distinct attention.

Origins and terminations.—The optic nerve is then, though for a long time the contrary has been believed, a mixed nerve tract. From this fact its section produces complicated effects, of the same nature as those following the section of a tract of the spinal cord. This section, in fact, cuts simultaneously elements, some of which are centripetal and others centrifugal, and which consequently proceed in opposite directions, their trophic centres being, the first in the retina, and the second in the encephalon. After this section, the terminal segments undergo Wallerian degeneration, while the cells of origin are the seat of that of Nissl. *For the centrifugal fibres the Wallerian degeneration is continued towards the retina ; the degeneration of Nissl affects, in birds, the cells of the third layer of the optic lobe,* which are thus termed *trophic centres,* or cells of origin for the centrifugal elements of the optic nerve. *As regards the centripetal fibres the degeneration of Nissl affects the ganglionic cells of the retina, while the Wallerian degeneration will be propagated* through the chiasma *towards the optic lobes* (bigeminal tubercule) whose whole investment of white matter disappears, in so far as it represents the termination of the optic fibres. The neurons which leave the optic lobe to continue these fibres, and whose cells of origin are situated in these lobes, feel the rebound caused by the disappearance of the optic fibres and the resulting lack of stimulation for themselves. They do not suffer degeneration properly so called ; they persist, but become atrophied (atrophic degeneration, functional atrophy) (Jelgersma).

What is their function ?—As experiment under the circumstances is an impossibility, it seems natural that the imagination should be exercised in order to find them a probable function. At the same time, however daring the hypotheses formed in such cases may be, they only tend to generalize former experiments, and this is what has taken place here. The first known type of the nerves

called centrifugal was the motor nerve, which causes the contraction of the muscular fibre. It was supposed that nerve cells at whose contact these centrifugal fibres spread out their ultimate ramifications, without being muscle, possessed at any rate one of the properties of the muscular element, namely, contractility. These contractile nervous cells would, according to the disposition of the impulse transmitted to them, either establish certain contacts between retinal elements, or else cause the cessation of these contacts, by an alteration in the distribution of the currents of stimulation in the nervous retinal network and the centres following it.

This hypothesis errs not by excess, but by want of width of scope. It appears to assume that the motor nervous system only controls the massive movements or mechanical phenomena of the living being; while in reality it exerts a general control over the molecular movements or chemical phenomena of the protoplasm: as proof of this may be brought forward the nerves which cause the glands to secrete for the formation of special products in the centre of their cells. These centrifugal fibres, which, according to histology, only proceed to nerve elements, necessarily excite molecular movements in these elements in connexion with their special function. What is this function? We can only answer that for the present it is impossible to tell. To consider it as exclusively of a mechanical order would be arbitrarily to narrow the fields of possible suppositions whose number, apart from experiment, is, so to speak, unlimited.

How is it possible to be sure that these nerves, whose function is unknown, are centrifugal?—The proof given is merely embryological and morphological, nevertheless it appears convincing. All neurons have two poles which appear under the form of two ramified extremities of whose arborizations some collect the impulses (initial pole), and others distribute them to the contiguous elements (terminal pole), and we are able to distinguish these poles by certain morphological characters (relations with the cell). When we see in the optic nerve neurons (few in number it is true) having their cells situated in the encephalon, and their axis-cylinder arborizations in the retina, we say, without hesitation, that these nerves are centrifugal and know we cannot be mistaken.

Nervi nervorum.—This very unexpected arrangement of centrifugal nerve elements terminating in a sensory nervous organ suggests, as we have seen above, the hypothesis of the existence of an entirely new class of nerves guiding the function of other nerves, which has been designated by the name of *nervi nervorum*. It is to be feared, however, that this appellation will tend to obscure the question instead of simplifying and elucidating it. The designation of *vasa vasorum* has been bestowed on the small vessels which the circulatory system distributes to itself to nourish the tissues added to its internal membrane, this being from the vascular point of view the only essential function, and of which the coronary arteries irrigating the myocardium are one of the most striking examples. We may also by analogy give the name of *nervi nervorum* to the nerves sent by the nervous system to its own special coverings, such as the dura-mater, for the performance of the sensory or even obscurely motor functions of these membranes, and indeed to any portion included in the nervous system which is not itself of a nervous nature (protoplasmic movement of the fixed cells), but

here the comparison which so far may be considered justifiable must stop.

The fact that nerve elements are governed by other nerve elements has long been known. The nervous tissue is an organized system, whose different portions communicate the impulse to themselves in a determinate direction. According to this the sensory nerves which bring the motor nerves into action for the performance of a reflex act would be *nervi nervorum ;* but this is not what is implied by the new expression.

The signification of the centrifugal fibres having their termination in the sensory elements.—Nevertheless, it must be universally felt that the new data brought forward through the knowledge of these fibres, up to the present time considered as being aberrant, is very important, and here is the interpretation I put upon it. The scheme of the organization of the nervous system which has so far held good, is that of a circuit, a circulation of impulses of which the reflex act gives a good idea. This circuit is generally regarded as being open towards the periphery ; this, however, not being usually true, since in a number of reflex acts the movement produced becomes again the cause of stimulation for a movement of the same nature (see *Respiratory Automatism*). It is also known that this circuit, which was always previously supposed to leave the periphery and to return there, in reality is sunk more or less in the depth, the locality of reflexion being, for example, sometimes in the ganglia, sometimes in the spinal cord, and sometimes in the brain, according to circumstances. The centrifugal fibres of the optic nerve would give us cause to *imagine the individually completed existence of reflex circuits*, whose starting-point and place of arrival are not necessarily at the periphery, but situated in certain localities of the grey matter, that is to say, in the nervous system itself, at variable depths.

Development and excitability of the cortex of the visual sphere.—In an animal at the moment of its birth, the cerebral cortex is generally not yet excitable ; which is as much as to say that electrical stimulation brought to bear on the Rolandic region does not provoke the well known muscular reactions usually obtained (Soltmann). This excitability of the cortex is only apparent after a number of days, which varies according to the animal. Further, the appearance of excitability also varies according to the region or cortical spheres under stimulation. In the dog excitability of the tactile area (Rolandic area) only appears towards the tenth day ; in the guinea pig, it exists from birth.

In all concerning the visual sphere excitability hardly exists in the dog before the fortieth day. On the other hand it has also been proved that it is only at this date that the animal is capable of following or

seeking with the eyes the object presented to it, or that it wishes for.

These two facts, one of observation and the other of experiment, are in agreement and explain each other (Steiner). If in the dog development of vision be followed from birth, it will be seen to pass through the following phases : at first the eyes are shut ; towards the twenty-fifth day they open ; nevertheless, in spite of the eyes being open, the animal is still blind, as it cannot avoid objects placed counter to it. Towards the thirty-fourth day it avoids these objects, but does not see them unless they are placed in the direction of the visual axes ; it is incapable of any movement of the eyes to seek them. These movements, however, appear after the fortieth day, and their appearance coincides with the development of the motor excitability of the visual area.

In the same animal, hearing and especially smell, have an earlier development.

In other animals, development of motor excitability in the visual area is also delayed behind that of the motor area, although the periods of this development are, speaking generally, very different for each of these areas. Thus, in the cat and the rabbit excitability of the visual area appears towards the fifteenth day, five days later than that of the Rolandic area.

The more perfect a function, so much the more will its complete development require time for its evolution. We may thus explain the differences observable between one area and another in the same subject, and also between the same area in different animals and even in different individuals.

In an infant it is only from the fifth week that the eyes are fixed on objects coming into the prolongation of the visual axis. It is only at the fifth month that the infant follows with the eyes or seeks with them for objects situated or moved about before him (Rahelmann). According to all probability, it is then, and only then, that his visual cortex would be found to be excitable, if it were possible to examine it electrically, as in the preceding experiments

CHAPTER III

AUDITORY INNERVATION

Of all the specific innervations, auditory innervation is perhaps the highest and the most perfect : it is far from being the best known ; but the sense of hearing in the human species appears to acquire in connexion with the function of spoken language (which all men possess) an importance even exceeding that of the sense of sight. Again, in this system there is a differentiation marked by a dissociation between an element common to all sensation, the idea of exteriorization, or, to put it better, of exterior localization, and the conception of specific sensation, which is here audition properly so called.

Comparative anatomy and physiology.—Embryologically the auditory apparatus is, like that of the other senses, derived from the ectoderm. Functionally, it is a transformation of the tactile apparatus adapted to the analysis of pressures and of special movements. We see it gradually advancing towards the specific form it possesses in the superior vertebrata. Further, it retains even in them, first traces of its tactile function. This function has remained visible more especially in the vestibular portion of their labyrinthine apparatus, the origin of which is far older than that of the strictly auditory portion.

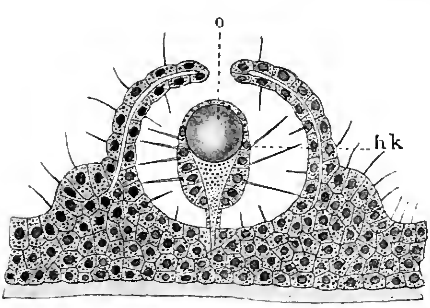


Fig. 239.—Auditory organ of the Rhopalonema still showing a small orifice (Hertwig).

hk, modified tentacle ; *o*. auditory organ.

In the *cœlenterata* this apparatus is roughly sketched under the shape of a vesicule constructed of neuro-epithelial cells which contains internally a solid mobile mass—the otolith. In *Medusæ* the otocystic formations known as auditory vesicules appear, with ciliated pavement cells facing internally, connected by nerves to a nerve ganglion, and this in its turn to muscles : the reflex sensorial arc is already formed (Beaunis).

Such is the primordial apparatus, which in invertebrata may present fairly diverse forms (open or closed vesicule, single or multiple otolith, etc.), and to which elaborated portions tend to be added.

In *fish* the ear is composed of a labyrinth with a central cavity or vestibule, possessing an utriculus and three semicircular canals, but no cochlea.

In *snakes* a rudimentary cochlea appears, but is, however, reduced to a quarter of a turn. In these animals the cerebellum is very little developed.

In *birds* the semicircular canals are highly developed, the cochlea generally remains rudimentary, but the cerebellum assumes a somewhat high development.

In *mammals*, the auditory apparatus is complete as in man. The vestibule communicates on one hand with the semicircular canals, and on the other with

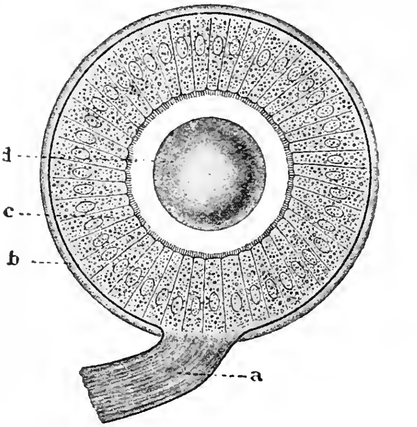


Fig. 240.—Otocyst of Unio.

a, acoustic nerve; *b*, capsule of the otocyst in which it ramifies; *c*, vibratile epithelium; *d*, otolith.

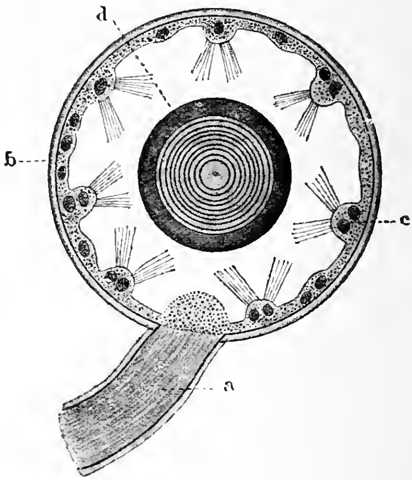


Fig. 241.—Organ of hearing in Barinaria.

a, acoustic nerve; *b*, epithelium of the otocyst; *c*, ciliated papillæ (auditory hairs); *d*, otolith.

the cochlea. The sonorous waves in them, having become aërial, are propagated to the internal ear through a cavity (middle ear), after having been condensed by a trumpet (external ear).

Labyrinth.—The aggregation of cavities forming the internal ear is the labyrinth. Here may be distinguished a middle portion (vestibule) communicating with two other series of cavities (semicircular canals on the one hand, cochlea on the other). The vestibule contains two orifices closed by elastic membranes, which form a mobile separation between it and the cavity of the tympanum. This assemblage of cavities is filled with a liquid (perilymph). Any pressure brought to bear on one of these two membranes will cause this liquid to oscillate by depressing one while the other undergoes an opposite movement. This is precisely what is done by the chain of ossicles which by its ultimate portion (stapes) is attached to the membrane of the fenestra ovalis and transmits to the ossicles the movements of the membrana tympani which is caused to vibrate by the contact of the sonorous waves.

The osseous labyrinth is throughout lined by a soft membranous investment, the membranous labyrinth, which is exactly adjusted to its cavities and is filled with liquid (endolymph); it is separated from the osseous wall, to which it only adheres at the site at which the nerve fibres penetrate, by another fluid (perilymph), in such a way that the whole system is filled by these two layers of liquid, which are capable of influencing each other mutually through the thin membrane which separates them. It is this membrane which transports to certain special localities the ciliated nerve terminations which collect the excitation.

The liquid current thus produced in the vestibule is conveyed in the cochlea and in the semicircular canals. The characteristic structure of these organs impart to the impulse special directions and movements. The cochlea is, as

its name indicates, a cone rolled, as it were, on its axis ; but this cone is double, being divided by a median partition into two parallel scalæ communicating above, of which the bases or inferior orifices open, the one into the vestibule towards the fenestra ovalis (scala vestibuli) and the other towards the fenestra rotunda (scala tympani). Thus the liquid in its undulatory movement through the cochlea has the benefit of a double route through the latter. Between the two scalæ, incompletely separated the one from the other by the lamina spiralis, a third of a membranous nature formed by the prolongation of the membranous labyrinth is found, which, in the semblance of a slightly flattened internal tube, completes the partition formed by the lamina spiralis. This is the membrane of Corti, in which the ultimate branches of the acoustic nerve come to an end. This mobile layer receives the rebound of the undulations of the liquid and transmits it to the extremities of the nerves contained in it. It collects them in its different portions according to the pitch of the sound (Nuel, Bonnier). Shrill sounds will take origin towards the base of the cochlea, and deep sounds towards its summit.

In the vestibule itself, in the saccule, the wave resulting from the displacement of the liquid strikes the crista acustica. This is the name given to projecting portions of the saccular membrane which are provided with cilia, and also furnished with nerve terminations. Placed in opposition to the liquid current, like a kind of dyke which may also be submerged, they receive from it an impulse which is strengthened by the displacement of the otocones, these being a sort of dust or grit of extreme tenuity which is agitated by this liquid.

Finally, there is an ebb and flow at the orifices of the semicircular canals, and therefore currents which pass through them ; these currents are also a source of excitation for the nervous currents ending therein.

A. LABYRINTHINE EXCITATION

The excitation we call auditory is of a complex nature : it conveys to us, in addition to the specific tonal sensation of hearing, other unconscious or subconscious impressions which play a most important part in the formation of our idea of space. From this point of view audition may in a certain degree be compared to touch, in which, together with cutaneous sensibility, a less distinct sensation of deep origin which is called the *muscular sense,* is associated ; but in auditory innervation the specialization of the two functions, that is to say, the dissociation of the idea of space from the specific sensation is carried a great deal farther.

Uniform modality of the excitation.—The three apparatus, of such very distinct geometrical form, composing the internal ear, or labyrinth, all receive the impulse in a similar manner, and the method originates in tactile excitation by contact or by rubbing. An aërial wave causes the tympanic membrane to vibrate ; it is transformed into a solidarized movement of the chain of ossicles, it gives rise to a displacement and liquid currents in the labyrinth, and the nervous papillæ of the latter, analogous to those of the dermis, are stimulated. It must be admitted that this form of stimulation is more comprehensible than that suggested by Helmholtz, which attributes to fibres of

microscopic dimensions the possibility of vibrating separately, according to their length, in conformity with the pitch of the sound emitted.

Different appropriations.—This uniform method of excitation of the nerves of the ear by external pressure, alternately positive (condensing wave) and negative (rarefying wave) is utilized for the purpose of effecting different analyses in each part of the labyrinth. In the cochlea, the collected impulse determines the auditory sensation. In the semicircular canals, the impulse is united to the notion of direction or sense of space. In the vestibule the nature of the impulse is in some degree of a mixed character, and participates in that of both the preceding.

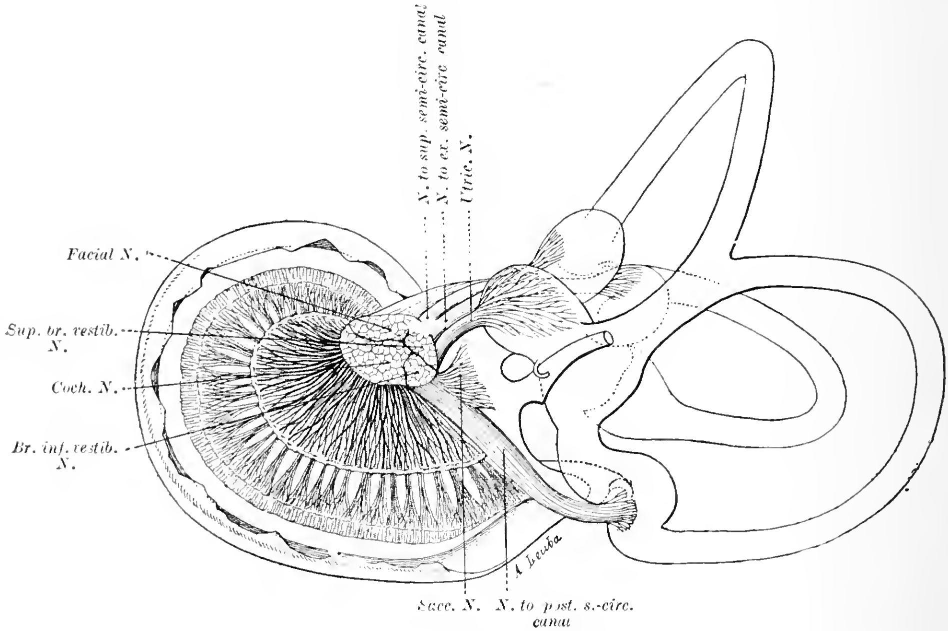


FIG. 242.—Mode of ramification of the auditory nerve (after Retzius). Right membranous labyrinth, seen posteriorly.

Far from being limited to hearing alone, the apparatus we call auditory furnishes us with varieties of information other than those by which it analyses sound ; it possesses, as it were, a certain number of secondary functions derived from its method of excitation, such as has been explained above. Bonnier attributes to it the following functions in particular :—

Baresthetic function.—By it the animal, whatever be the species, under consideration, possesses the power of estimating the pressure exercised on it by the external medium, be it aërial or liquid, in which it lives.

The liquid (perilymph and endolymph), shut up in the closed cavity, or rigid portion of the labyrinth, has no tension of its own in this cavity, but arrangements exist there which ensure it (normally) equality of tension with the external medium. Thus it will reflect, either the constant state of this pressure, or its variable conditions (during shocks). It is true that there are canals of derivation,

but these are too delicate to allow of the exit *en masse* of the labyrinthine lymph, but on the other hand they are sufficient to re-establish compensation when the difference of tension becomes too strong. Other protecting mechanisms, like the muscle moderating the pressure of the stapes on the fenestra ovalis, are also adapted to diminish the effects of exaggerations of external pressure and so preventing the rupture of the membranes of the labyrinth which would ensue. However that may be, we possess an apparatus which instructs us with regard to the state of external pressure and its variations.

The resulting sensations are not conscious ones, they only become so when reaching a condition of discomfort approaching pain, or indeed of pain itself. They nevertheless act on us as a source of internal excitation and may modify our general aptitude.

Manæsthesic function.—If the internal pressure of the labyrinthine lymph

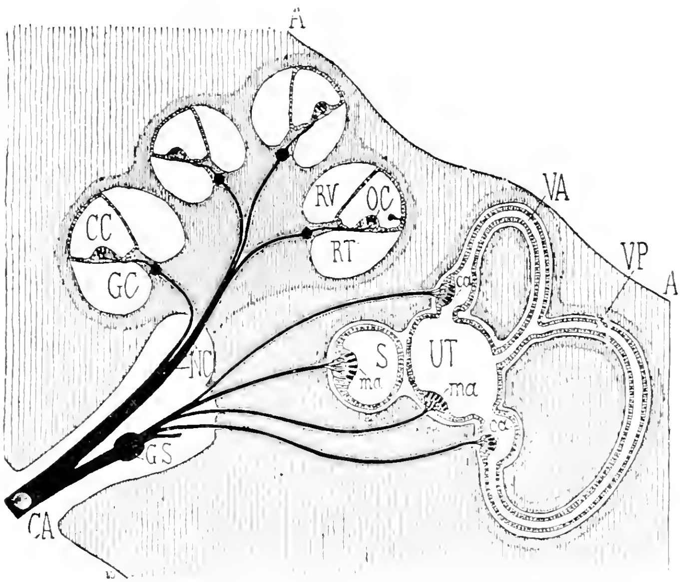


FIG. 243.—Diagram of the internal ear.

RT, scala tympani; RV, scala vestibuli; CC, cochlear canal; OC, organ of Corti situated on the basilar layer which separates the scala tympani from the scala vestibuli; GC, ganglion of Corti in the canal of Rosenthal; *Si*, saccule; UT, utricule; VA, anterior semi-circular canal; VP, posterior semi-circular canal; *ma*, auditory maculæ of the utricule and saccule; *ca*, auditory crests of the ampullæ of the semi-circular canals; GS, ganglion of Scarpa. It has not been possible to represent the horizontal canal which is perpendicular to the preceding (after M. Duval).

(which has its immediate source in the pressure of the arteries distributed to it) becomes in certain conditions too high, the internal ear acts as a plethysmograph and its sensory nerves register this pressure according to its conscious or unconscious manifestation and also its degree. The liquids of the labyrinth (perilymph and endolymph) are not humours of a permanent nature, but like all analogous liquids are submitted to a slow circulation which renews them. Produced in the canals by secretion of the endothelium which lines the latter, they are suspended in the lymphatic spaces of the dura-mater and the subarachnoid membrane.

The equilibrium between their production and distribution is regulated by a reflex vaso-motor and secretory excitation, which is itself regulated by the pres-

sure. Disturbances of this mechanism, as regards any of its factors, will induce abnormal variations of the internal labyrinthine pressure with its consequences (buzzing in the ears, vertigo, nausea, vomiting, etc.), which are caused by reverberation of the sensory excitation either on the bulbar nuclei or others.

Seisæsthesic function.—The abrupt and rhythmic variations of the pressure of the external medium are also registered in the internal ear like the preceding, which we have, in the first instance, supposed to be slow and isolated. This will be the same excitation become periodic.

a. *Vestibule.*—This seisæsthesic function which registers the vibrations of whatever kind appertains to the vestibule, and more especially to the utricule. Its membrane (fenestra ovalis), shaken by the stapes, communicates its vibrations to its liquid, and by it to the crista acustica. The resulting sensations are not hearing, properly so called, but a phenomenon which is prepared there and which will become hearing in the differentiated apparatus of the cochlea. These sensations are the

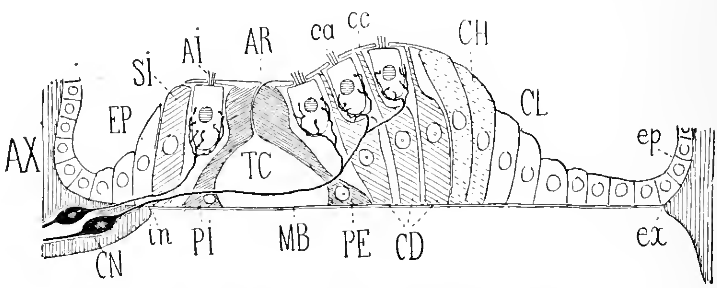


FIG. 244.—Structure of the organ of Corti.

AX, axis of the cochlea; MB, basilar membrane; *in*, its insertion in the free border of the spiral osseus membrane; *ex*, its external insertion: TC, tunnel of Corti; PL, its internal pillar: PE, its external pillar; AR, articulation of the two pillars.

AI, internal ring, giving passage to the hairs of the internal acoustic cell; SI, cell of external support; EP, indifferent epithelium; CD, cells of external support forming by their prolongation the articular membrane *cc* whose orifices give passage to the cilia *ca* of the external acoustic cells or those of Corti.

CN, cellular bodies of acoustic neurons, situated in the canal of Rosenthal (ganglion of Corti). One of them has its receptive arborizations in an internal acoustic cell; the other in the external acoustic cells (after M. Duval).

hearing of the invertebrata or, at any rate, in them take the place of hearing. They are very general, and may be found in man. It is these which, in a deaf person deprived of cochlear audition, permit him to perceive the vibrations of a tuning-fork placed on the skull or on the mastoid apophysis (Bonnier).

b. *Cochlea.*—The function of the cochlea is very complex and its mechanism is still obscure. In embryological and functional development it is the last to put in an appearance; it is the most differentiated and most conscious portion of the auditory apparatus taken as a whole, and for this reason it disguises the others, which can only be revealed by an analysis external to the subject itself. We shall examine it in a

special manner with regard to the senses properly so called and their organs. The cochlea also collects vibrations whose mode of origin and propagation is not essentially different from that of the preceding.

These vibrations are fused together in the nervous system, which contains their initial expansions. They give rise in it to a continuous sensation which is called the *sonorous* sensation. This consequently proceeds from a periodic repetition of the excitation and is only brought into being when the rhythm is comprised between certain limits, the one minima (32) and the other maxima (76,000 vibrations to the second). In music hardly any sounds are employed except those comprised between 40 and 4,000 oscillations.

c. *Semicircular canals.*—The semicircular canals make their appearance in the zoological series long before the cochlea ; they are a much less marked differentiation of the tactile sense than is the latter. They are found in the lamprey and the myxinodes ; they are highly developed in fishes. In man and the larger number of the vertebrata they exist to the number of three, *orientated in three planes which recall the three directions of space :* one is vertical and superior, that is to say, raised above the two others; it is perpendicular to the crest of the petrous portion ; the other is vertical and posterior, it is parallel to the axis of the petrous portion ; the last is horizontal and external. The three canals are perpendicular the one to the other reciprocally. At their point of communication in the vestibule these canals present ampullary dilatations, at the site of these dilatations their membrane presents a ciliated epithelium and a neuro-epithelium in connexion with the ramifications of the vestibular nerve. We have already said that these canals receive their portion of the excitation produced by the aerial wave which, by the play of the tympanic membrane and the ossicles, displaces the labyrinthine lymph. This excitation, which never gives rise to the sonorous sensation, is utilized for furnishing the subject with ideas of another description relative to his attitude, and his orientation in the surrounding medium. These ideas are related to what is known as the sense of space.

2. The Sense of Space

The relation of the semicircular canals to equilibrium was first noticed by Flourens in 1824. Goltz, Breuer and others, when repeating these experiments endeavoured to give a rational explanation of this relationship. De Cyon, in 1874, was the first to speak of a sense of space and connected with the more general conception of such a sense all the different experiments, including his own. In the midst of discussions and criticisms, the new idea gained ground and the expression

held good. The question was taken up by M. Duval and Laborde, and a number of foreign authors, Ewald being amongst them. It is to Bonnier that we owe the best analysis of the phenomenon of the formation of images in space and the most lucid outline of this complex question.[1]

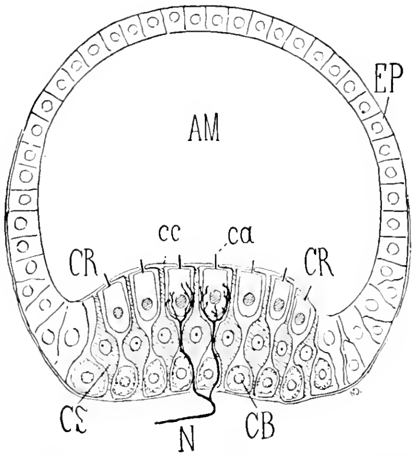


FIG. 245.—Diagram representing ampulla of a semi-circular canal and acoustic crest. (M. Duval).

AM, ampulla ; CR, its acoustic crest ; CB, basal cells ; CS, cells of support ; *cc*, cuticle ; *ca*, acoustic cells and their cilia ; N, nerve fibre going to the acoustic cells.

1. **Excitations of extrasomatic origin—Exteriorization and localization in space.**—We possess the faculty of distinguishing the origin of the aërial waves which reach us and which we call sonorous, in virtue of the sensation developed by them in a specific portion of our nervous system. We experience a sensation and, as in all the other senses, we exteriorize and localize in space the original cause of the impression and sensation experienced. The process of localization is a complex one, but its principal mechanism is contained in the semi-circular canals, or, in other words, in an apparatus annexed to that of audition, but distinct from it.

According to the direction of the aërial wave, the tympanic membrane is not affected in the same manner nor on all the same points of its different diameters. The transmission of movement to the fenestra ovalis, which is a genuine internal tympanum, is modified by it, and the attack on this membrane is concentrated on different points of its surface, whence arises a displacement of the labyrinthine lymph, this also taking place in different directions, so as to affect in a predominating manner, either the different parts of the crista acustica (in the saccule), or, more especially, the different semicircular canals. Thus we obtain particular indications with regard to the source of the aërial wave, and therefore of the sound heard (Bonnier).

2. **Excitations of intrasomatic origin.**—But the semicircular canals are also accessible to another kind of excitation independent of all pressure or any modification of pressure of the external medium (aërial or liquid). Goltz maintained that *changes of position* of the head in-

[1] P. BONNIER, *Le vertige* (Bibliothèque Charcot-Debove).

fluenced the distribution of the liquid in these canals and became the cause of the sensations by which equilibrium is regulated. Breuer defined this conception by pointing out that the labyrinthine lymph (endolymph), by virtue of its *inertia*, exerted a *friction on the sensory wall* of the ampullæ when the head was moved. Some variations of this explanation attribute the excitation of the ampullary nerves to a *counter-pressure* (but without displacement or friction) *of the lymph against the wall* in a direction contrary to the displacement, or else to some irritation of an unknown nature, but probably connected with *acceleration*. According to Breuer, Mach, Crum-Brown, the semicircular canals are the organ of sensations of acceleration.

Relation between the direction of the movement and that of the semicircular canals.—Previously to all these explanations Flourens had demonstrated (1824), by very striking experiments, the strict connexion which unites the semicircular canals to the co-ordination of movements, and consequently to equilibrium. *Separate section of each of the canals produces disorderly movements, in the direction of the plane of the mutilated canal.*

Pierret, Brown-Séquard and Bechterew have shown that these disorders may also be observed in lesions of the labyrinthine nerve.

Cyon does not consider that the movements of the liquid or the liquid itself cause stimulation of the ampullæ. He brings forward as an objection the viscosity of this liquid in a tube of capillary dimensions, and the fact that its escape, after the opening of the labyrinth, does not produce a loss of equilibration. The locomotory disturbances brought about in the experiments of Flourens would be due to an excitation, not to a paralysis (Loewenberg). The destruction (though certainly complete) of the semicircular canals does not cause these disorders (Steiner), this being in favour of the lesions acting as an excitant. At any rate, lesions of the cochlea bringing deafness in their train do not disturb the equilibrium. The starting point of convulsions is in lesions of the ampullæ rather than in that of the canals, that is to say, in the locality which contains the nerve arborizations (Lussana).

Unconscious sensations.—A point about which there is room for insistence is that impressions and sensations having this origin are not conscious (at least not habitually conscious), but are connected with reflex acts which, by being exaggerated, in lesion of the canals become convulsive (Loewenberg, Laborde).

3. **Link between the muscular tonus and the motor power.**—The relation between the semi-circular canals and muscular movement is a close one, and displayed in a very evident manner to all observers.

R. Ewald maintains that these organs are the starting-point of con-

tinuous and permanent impulses, reflected by the nervous system on to the muscular tissue ; so much so, that after section of the labyrinthine nerve or destruction of the canals, muscular relaxation is immediately produced, and displayed by loss of tonicity, and inability in the animal to perform energetic movements. In fact, *the animal preserves its muscular energy, but no longer knows how to employ it.*

H. Girard has, it is true, remarked in the frog, after unilateral section of the acoustic nerve and destruction of the labyrinth, the reflex excitability of the corresponding side to be increased.

This connexion of the labyrinthine apparatus with motricity is also defined in the experiments of Cyon, who shows that there is a determinate relationship between the excitation of each canal in particular, and the movements of the eyeballs. And these relations are such that the movement produced (by a reflex path) corrects, or tends to correct, the visual illusion which arises from the movement provoked. And a relation of the same nature would also exist with the locomotor muscles (Y. Delage).

4. **Analysis of the perceptions of space.**—Whatever idea may be formed with regard to the modality and nature of the excitations collected by the semicircular canals, the relation of this apparatus to the position of the body and the sense of space cannot be denied. The wave, whatever it may be, which reaches the three canals taken as a whole, will have on each of them, by reason of the relative arrangement of their planes at right angles, an unequal action on each of the three, and one which differs according to its own direction. The idea of this direction is drawn from the comparative value of the excitations produced on each of the three canals. The movements of the head in different directions, changes of place in the body as a whole, are equally as regards the different canals both right and left, the origin of equal, unequal, or inverse excitations, which give us information with regard to changes of position of the head or body, and also concerning the movement of the latter, and any acceleration of this movement.

By the muscular sense, or that which has been more correctly called the cinesthetic impressions, we are instructed with regard to the relative displacements of our limbs and their segmentary positions ; from the sensations produced by the semicircular canals we receive information with regard to changes of place in our bodies and its attitudes, in connexion with the surrounding medium. In that special sense which has been called the sense of space, a preponderating position is taken by the apparatus called auditory, and it owes this to an organ distinct from that which collects sounds ; still this position is not entirely exclusive. Touch procures information of the same nature with regard

to objects in immediate contact with us. Sight furnishes us with it for distant objects. Between these two senses and the ear the difference is that localization of the exciting cause is in the latter made by the sensorial apparatus itself, and not by an apparatus other than the sensorial. The retina at the same time sees and localizes objects (*visual sense of space*); the skin gives us the idea of contact and also of the position of bodies (*tactile sense of space*). In the ear the cochlea hears, and the semicircular canals localize the sound heard (*auricular sense of space*, which by some is considered as the only sense of space).

5. **Superposition and synthesis of notions of space furnished by each sense.**—Thus, wherever there is exteriorization and localization of the originating cause of sensation, there is an idea or sensation of space. *Each sense, in different degrees, is a sense of space;* further, each sense duplicates this common and primordial idea of specific sensation; that is to say, one which is irreducible to the sensation belonging to the other senses. *It is by their spatial element that these ideas are superposable.* It is by the superposition of these ideas that we identify the objects of which different senses display to us the various qualities (Bonnier). It is by successive identifications that we pass from the sensation to the idea, and the vocal or graphic sign expressing it, then from the simple to the general idea, from the concrete to the abstract.

Objective and subjective orientation.—The perceptions which maintain the sense of orientation are of two orders, or at least may be classed under two headings. The first give us information concerning the situation of objects and their relations with us and with each other, and variations in these relations, that is to say, their movements or changes of position; they are furnished to us by those senses which, like sight, touch, and even hearing, being open to the external world, receive shocks either directly or indirectly of *extrasomatic* origin, and which are gradated, as indeed are these objects themselves; this is *objective* orientation. The second instruct us concerning the position of our bodies with regard to these objects and to changes in this position: they reach us, in a great measure, from an apparatus to which the sense of hearing is as it were annexed, the semicircular canals and the utricule which are arranged so as to collect excitations of *intrasomatic* origin from the fact of the movements, or only from the attitude of our body: this is *subjective* orientation (Bonnier).

The distinction between objective and subjective is here, as may be seen, drawn, not from the physical or psychical nature of the phenomena, but from the anatomical and functional difference between the receptive apparatus of the senses. This division, however, is not absolute, since the labyrinth itself is capable of giving us information with regard to the direction of the shocks coming to it from external objects, and hence of their situation, and, on the other hand, deep tactile sensibility also instructs us concerning the relative situation of our organs and limbs.

The labyrinthine apparatus is constructed so as to furnish us with a faithful analysis of the movements (and even the positions) of our body with regard to the three dimensions of space. But these three dimensions are not selected

arbitrarily. There is at least one of the three, the vertical, which is given by weight, and which represents a force or excitation at a distance, defining the position of our body with regard to the earth supporting us ; so that subjective orientation is itself, as it were, slightly tinctured by objective orientation. Fundamentally, objective and subjective orientation preside over each other mutually, as do action and reaction, and the disturbance of one may bring about that of the other.

Vertigo.—Vertigo is defined by Bonnier as being a disturbance of subjective orientation, supervening either directly or indirectly. Like so many others, the function of orientation can only be correctly exercised by means of reciprocal links between sensibility and movement ; whence it follows that vertigo includes both sensory and motor phenomena which, taken separately, would not be sufficient to characterize it. In all concerning sensibility, vertigo may, like orientation itself, be either conscious or unconscious. However, speaking clinically, it is by the special sensation, *sui generis*, accompanying it that it is habitually characterized ; whence the definition of Grainger Stewart accepted by Weill: vertigo is " the feeling of the instability of our position in space relative to surrounding objects. In reality, vertigo may exist without consciousness of giddiness, unconscious orientation (the most usual) being capable of disturbance like conscious orientation (more exceptional).

Forms of vertigo.—There may be vertigo from want of perception of space (momentary suspension of all conscious localization), from too acute perception of space (vertigo of heights, agoraphobia), from illusion of space (illusion of position, direction), or from hallucination of space (obsession of an unreal void, or unreal movement or position). (See Bonnier, Vertige, *Bibl. Charcot-Debove*).

Different origins of vertigo.—The sensorial apparatus which, like those of sight, of touch, and especially the semicircular canals, furnish the most important information for the guidance of the function of orientation, may by the disturbance, and therefore the discordance of their operations, become the exciting cause of vertigo.

Optical vertigo.—Weill enumerates a series of circumstances which may produce optical vertigo, principally, however, in neurotic subjects : abrupt transition from darkness to light or conversely (Purkinje), sight of numerous colours running into each other, or of material ornamented with lozenges giving the illusion of movement, passing in front of a railing, sight of running water, or of a rotatory body, etc., etc.

Labyrinthine vertigo or that of Menière.—Menière was the first to observe a very well characterized form of vertigo, having as a starting-point alterations in the internal ear and especially in the labyrinth. It must be noted that people born deaf are but little subject to vertigo or to sea-sickness.

Vertigo of tactile origin ; mixed vertigo.—The sense of touch takes part in many ways in orientation and equilibration. Weill gives proof of the existence of a vertigo of the muscular sense. An excitation which has its starting-point in a single sense, often in the restricted locality of a single nerve trunk, may spread by being propagated to the neighbouring sensory or sensorial nuclei (nuclei of the vestibular nerve) ; whence arise many forms of vertigo having a starting-point in the stomach, the nasal mucous membrane, the pharynx, the heart, the ureter, etc., and whence also are produced many external and internal motor reactions (palpitations, nausea, etc.) accompanying vertigo. Finally, the excitations may have many origins, as in the naupathia of sea-sickness (see Weill, Des vertiges, *these d'ag.* de Paris, 1886).

Not only may abnormal excitation have varied and numerous sensorial origins, but as regards the same sense functional alteration may have a varied place in the cycle, and affect the receptive apparatus, the sensorial conductors, the bulbo-

medullary nuclei, the cerebellum, and the brain, whence so many kinds of vertigo, *bulbar*, *cerebellar*, *cerebral*, etc.

2. Specific sensation or that of auditory tonality

1. **Auditory field.**—We have an auditory just as we have a visual field; and the former, instead of extending in front of us, as does the latter, is situated laterally, in the form of an extremely spread-out cone, whose axis is located in the prolongation of the auditory meatus, and whose base is external. We have in reality two auditory fields, one for each ear; but whereas the visual fields of both eyes are superposed so as to form but one, the auditory fields are diametrically opposed. Nevertheless, they partially overlap so as to fill the hiatus which they tend to leave either in front or behind. It is behind that this gap is most obvious; and it is at the back of the head that approaching deafness at first shows itself, and it is in the prolongation of the axis of the auditory duct that audition persists the longest (Gellé).

This orientation in an opposite direction of the auditory fields of the two ears gives rise to conditions which are special to binauricular audition and renders it very different from binocular vision. It suppresses certain of the advantages of the latter; but at the same time creates new ones. From the fact of the lateralization of a sound, in the exteriorization made for us by it, we arrive at some idea of its origin and of its localization in space. We guide ourselves by this indication; either by turning the head and the ear distinctly to face the sound, if we wish to hear it better; or, on the contrary, by turning the head and the eyes in its direction, if we wish to see the original cause of it; this is an act of voluntary motor, instinctive orientation (Gellé). This movement may be compared to that made by the eyes in order to locate the image of the objects on the central part of the retina. But, whatever be the direction of the head and the ear, and without the necessity of any change in their position, we have a means of recognizing the direction of the aërial wave which reaches us.

The apparatus which analyses the direction of the exciting wave is situated in the internal ear, the labyrinth, and especially in the semicircular canals (Bonnier). We have seen above how this analysis is performed and how distinct is the apparatus which analyses the direction of the wave from that which analyses tonality.

Binauricular audition.—Consciousness is *one* and alone; it is in every case the characteristic of our unity, that is to say, of our being. The excitations penetrating our nervous system, in proportion as they reach its depths, are synthetized into a sensory phenomenon which

does not allow of their component elements being longer distinguished, or, at least, which establishes no distinction except between their principal groups, and that generally only on the condition of an effort of the attention seeking for them in the field of consciousness. Sounds, even when they strike unequally on our two ears, give us but a single perception. This inequality in the intensity of the impression may, nevertheless, be in some degree perceptible, as it is pointed out by a motor phenomenon of orientation; only this perception is not usually of a distinct nature, but is obscure, resembling that which regulates reflex or automatic acts.

2. **Fusion of excitations into the sonorous sensation.**—When vibrations with a long interval between them strike the ear, they act as isolated excitations, and can be separately distinguished. When these vibrations attain a frequency of sixteen shocks or oscillations, we can still distinguish them, but can no longer recognize an interval of silence between them.

Thus the nervous system possesses the power of associating impulses in time, just as it has the power of associating the simultaneous stimulations of the two labyrinths and of the component elements of each of them. In proportion as the frequency augments, the fusion becomes more complete: sensation is continuous.

3. **Damping of the vibrations special to the ear.**—A movement applied to a body, should the latter be of an elastic nature, tends to communicate to it a vibration which persists after the shock, even if this be instantaneous and not repeated. This secondary vibration, were it permitted to exist, would absolutely falsify the information which the sense of hearing supplies. Special, but so far undetermined conditions, certainly exist in the labyrinth, whose effect is to damp this secondary vibration, so that only the primary vibration is utilized for the stimulation of the auditory apparatus. The viscous nature of the liquid which is displaced in tubes of capillary dimensions is a circumstance which may help to explain this phenomenon of the damping of the vibrations (Bonnier).

Thus conditions exist at the origin of the nervous cycle in the organ which receives the impulse which cause the movement received to possess exactly, or all events sensibly, the same value, not only with regard to intensity, but also as concerns duration, as the external movement communicated to it. But in the nervous system itself the excitation (transformed into a nervous wave) has a far more prolonged echo, whence arises the fusion of impulses succeeding each other with a rhythm of rather more than ten to the second, and the unity or continuity in time of the resulting sensation.

If a sound is too short, it is not (other things being equal) perceived below a certain duration (Gellé).

4. **Rate of development of the sensation.**—The excitation, in order to terminate in the psychical phenomenon of sensation, must be developed in the nervous system. This development, which implies phenomena of succession and association, which are at the same time both numerous and complicated, requires a certain time for its elaboration. Methods have been devised to determine this period of time.

The method is a general one. The shortest interval which elapses between the commencement of an auditory impulse and the motor reaction which answers to this impulse, is measured. Beaunis estimates this interval as being 106 to 159 thousandths of a second or, on an average, and in round numbers, 150 thousandths of a second. It may through practice fall to 100, say a tenth of a second. This delay is certainly longer than the time required for transmission along the course of a single nervous conductor. The impulse is delayed by the multiple and graduated transformations which take place in the grey matter, and especially by the cerebral transformations, an attempt having been made to separate these from other superposed transformations which are sufficiently well known. According to Richet, these cerebral transformations would require a half-tenth of a second.

When sounds possessing different characteristics (like the articulated sounds of speech) succeed each other, a certain interval between them becomes necessary in order that they may be distinctly perceived, that is to say, that their characters may be recognized. Richet, according to his own personal experience, estimates the rate of articulation of syllables, either spoken or thought, at ten in a second. It is this very rate which limits the perception of the words which we hear pronounced. The delay is of a psychical nature. It is also necessary that our attention should be awake, for a sound or a noise which takes us by surprise undergoes a much greater delay before arriving in our consciousness. This latter, however, once warned, rapidly discerns it should it be reproduced.

B. TRANSMISSION FROM THE EAR TO THE CEREBRAL CORTEX

The *acoustic* nerve, or that of the eighth pair, is formed by the union of two nerves, each arising from a special organ adapted to the reception of certain stimulations ; these two nerves are : (1) the *cochlear* nerve, which is stimulated by the displacement of a liquid filling the cochlea, these displacements being due to the pressure exercised by the vibrations of air or of sonorous bodies ; (2) the *vestibular* nerve, which is also stimulated by the displacements of a liquid filling the semicircular canals, which displacements are in this case due, not merely to the aërial waves arriving from the exterior, but also, and more especially, to changes of position of the head or of the body.

The cochlear nerve traverses, in the same way as the posterior roots, a ganglion situated at the base of the lamina spiralis, and is, like the latter, twisted (*spiral ganglion, or ganglion of Corti*).

The vestibular nerve also passes through a ganglion at the bottom of the internal auditory meatus (*vestibular ganglion, or that of Scarpa*). These two nerves are not entirely independent, for the cochlear nerve gives off a small branch to the saccule and to the ampulla of the inferior semicircular canal; the ganglion of this small branch lies at the bottom of the internal auditory meatus.

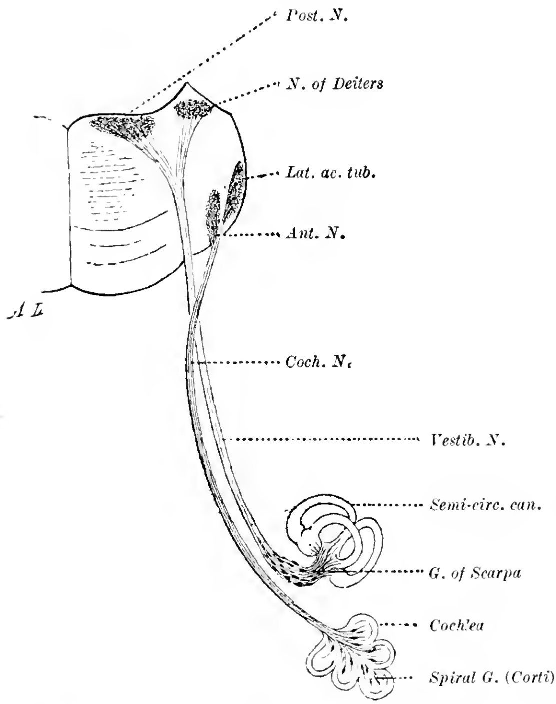


FIG. 246.—Origin and termination of the acoustic nerve.

Vestibular nerve.—The vestibular nerve has, like the posterior roots, two radicular branches; the inferior branch terminates in a grey mass situated immediately above the nucleus of Burdach, of which it is a kind of prolongation. The inferior radicular branch of the vestibular nerve is then in reality equivalent to the superior branch of the sensory nerves of the spinal cord, and this remark applies to the inferior radicular branch of the glosso-pharyngeal, a sensorial and sensory nerve, and also to that of the trigeminal and of the vagus, sensory nerves. The superior radicular branch (generally called superior root) of the vestibular nerve comes in contact in a very restricted space with three nuclei, called the *internal dorsal nucleus, the external dorsal nucleus* (*or that of Deiters*), *and the nucleus of Bechterew.* From these different nuclei fibres, called cerebellar, arise, which, with the help of the inferior cerebellar peduncle, reach the cerebellum either with or without decussation, where they terminate in the *nucleus of the roof*, the *nucleus globosus*, and the *nucleus emboliformis.* These fibres are obviously equivalent to those which, in the tactile system, form the cerebellar tract of the spinal cord. Other fibres, emanating from the primary nuclei (internal and external dorsal, and of Bechterew), and perhaps also from the nucleus of the inferior root, pass through the reticular formation, and after enlarging the fillet (riband of Reil) finally reach their destination in the cerebral cortex.

Thus the impulse, on leaving these nuclei, follows paths which convey it either to the brain, or to the cerebellum: further, there are some which from these same nuclei, and especially from the external dorsal nucleus, may convey it to

the nucleus of origin of the external oculo-motor nerve ; so that to the cerebral and cerebellar paths, reflex paths must also be added.

Cochlear nerve.—From the locality where the cochlear nerve comes in contact with the medulla oblongata by its lateral portion, up to the cortex, the acoustic cochlear paths traverse or skirt along a series of grey nuclei which are : (a) *the anterior nucleus*, and the *acoustic tubercle* (quite at the entrance), (b) *the nuclei of the trapezoid body* (either of the same, or of the opposite side after decussation),

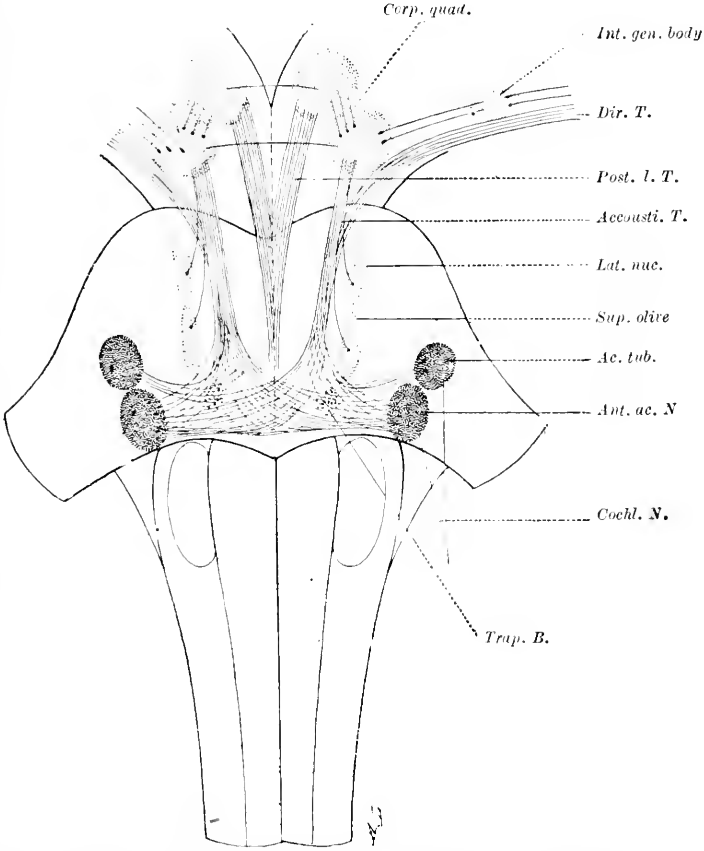


Fig. 247.—Diagram of the acoustic tract (central acoustic path of the cochlear nerve, Charpy).

(c) *the lateral nucleus of the fillet* (*riband of Reil*), (d) *the corpora quadrigemina* (principally the posterior), (e) *the internal geniculate body*, after which the fibres reach the cortex of the temporal lobe.

The fibres which either pass through or stop in these different ganglia are sometimes superficial, like the acoustic striæ, and the posterior arms of the corpora quadrigemina, and sometimes deep, like the trapezoid body or the fillet (riband of Reil).

We may add that the acoustic paths are also connected with the *optic thalamus*. This important organ is, in a manner, like the cortex itself, distributed between the different senses. The pulvinar is connected with vision ; between the pul-

vinar and the internal nucleus a segment is situated which is united by tracts to the temporal lobe, and which is connected with audition.

The presence in the course of the auditory paths of ganglionic masses, like the above-mentioned segment of the thalamus, the posterior corpus quadrigeminum, the internal geniculate body, all having such a striking resemblance to the ganglia passed through by the optic tracts (pulvinar, anterior corpus quadrigeminum, external geniculate body), establishes an obvious homology between the two sensorial systems and their principal relays.

The functional significance of these different nuclei would be of the highest interest, were it possible to ascertain it correctly, either by experiment, or even by comparison with the similar nuclei of the other senses. On this point positive data are almost entirely wanting. At the same time it may be observed that amongst these grey masses there are some which, like the *corpora quadrigemina*, are especially localities for *reflexion of the impulses :* the anterior corpora quadrigemina reflect the visual, the posterior the auditory impulses. The *other grey masses* are perhaps not entirely deprived of this power of reflexion, but instead of bringing back the impulse towards its starting-point, they seem rather to deflect it in the direction of the deep paths *leading to the cortex.* As they pass on, they associate the elementary impulses, and thus in a way sketch out the work of synthesis from which arises the specific sensation of audition, when these impulses, following a determinate order and connexion, shall arrive in the cortex.

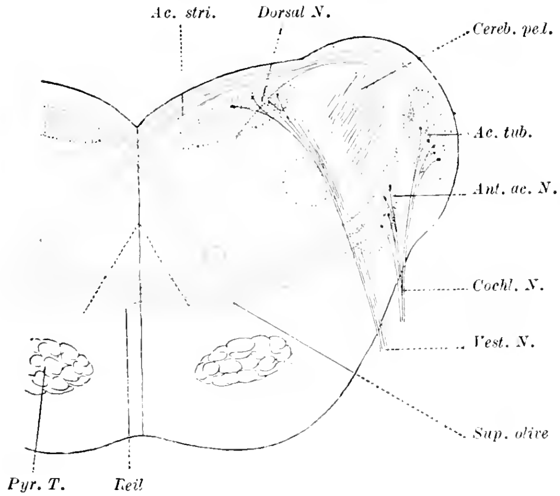


FIG. 248.—The acoustic striæ.

The striæ and the trapezoid body in blue. Transverse section of the pons. Diagrammatic (Charpy).

So far as can be ascertained, the general plan of these connexions between fibres is the same here as in the other senses. It is in principle maintained that in these fibrillary paths going from the ear to the brain, there is at least one break, and therefore at least two neurons transmitting the impulse. These breaks do not all occur in the same locality, but are graduated in stages on the different nuclei which succeed each other along the nerve path ; hence each nucleus presents terminal fibres and fibres of passage. Nevertheless, the fibres of passage emit collaterals which have practically the value of terminal fibres, so that the same neuron coming from the periphery distributes impulses to several nuclei. The neurons which, from these nuclei, proceed to the cortex are in general much more numerous than those coming from the periphery to them Further, between one nucleus and another, as between the elements of the same nucleus, there are longer or shorter neurons called neurons of association, whose part it is to solidarize and harmonize the elementary actions of the neurons conveying the impulses to these grey masses. Finally, in a certain number of these masses the impulse has to make a choice between two directions which are not merely dif-

LABYRINTHINE INNERVATION, KNOWN AS AUDITORY.—Chiefly its diagrammatic Systematization (after BONNIER).

	Sites of Origin.	Petrosal Tracts.	Nerve Trunks.	Ganglia of Origin.	Bulbar Roots.	Bulbar Tracts.	Primary Nuclei.	Sites of Termination.
VESTIBULE	Utricular macule.	1	VESTIBULAR NERVE.	*Ganglion of Scarpa.*	Anterior or Internal Root.	Direct Cerebellar Tract.	*Globular nucleus and that of the roof.*	CEREBELLUM. Direct tract. Crossed tracts. Internal nucleus. Internal nucleus and superior olive. Nucleus of Deiters (ascending root). Nucleus of Bechterew.
	Transversal ampullary Crest.	2				Crossed Cerebellar Tracts.	*Nuclei of the cerebellum.*	BRAIN. Lateral lobes. { Cerebellum. Red nucleus. Temporal lobes. { Superior olives. Corpora quadrigemina. Internal geniculate body.
	Horizontal ampullary Crest.	3				Descending root of Roller.	*Nuclei of Deiters and of Bechterew*	BULB AND SPINAL CORD. Facial and oculo-motor by the superior olive and the posterior longitudinal tract. Tympano-motor apparatus. Motor apparatus of the head and the limbs. Nuclei of the mixed nerves. Anterior acoustic nuclei.
	Saccular Macule.	4				Principal Tract.	*Internal Nucleus.*	
	Sagittal Ampulla.	5						
COCHLEA	Internal Ciliated Cells	6	COCHLEAR NERVE.	*Ganglion of Corti.*	Posterior or External Root.	Fibres.	*Acoustic Tubercle.*	BRAIN (temporal lobes). Acoustic striæ ; sensory tract of the peduncles. Anterior nucleus, trapezoid body, sensory fibres. Anterior nucleus, superior olive, trapezoid body.
	External Ciliated Cells.					External Fibres.	*Nucleus of Clarke.*	CEREBELLUM. Internal nucleus, superior olive.
	Cells of Deiters.					Fibres.	*Internal Nucleus.*	MEDULLA OBLONGATA and SPINAL CORD. Facial and oculo-motor by the superior olive and the posterior longitudinal bandalette.
						Large Tract.	*Anterior Nucleus.*	Psycho-motor and medullary motor apparatus by the cerebellum, the internal nuclei, the nucleus of Deiters.

MUTUAL RELATIONSHIP OF THE PRINCIPAL PRIMARY AND SECONDARY NUCLEI (after BONNIER).

Origins.	Terminations.
ANTERIOR NUCLEUS (or inferior)	Internal nucleus of the same side. Superior olive of the same side. Superior olive of the opposite side. Corpus quadrigeminum of the opposite side (by the trapezoid body). —Thence to the postero-basilar nucleus of the optic thalamus. —Thence also to the internal geniculate body, and by it to the temporal lobes.
INTERNAL NUCLEUS	Anterior nucleus of the same side. Superior olive of the same side. Nucleus of the roof of the same side. Nucleus of the roof of the opposite side.
GLOBULAR NUCLEUS	Cortex of the superior vermis.
NUCLEUS OF THE ROOF	Cortex of the superior vermis. Red nucleus of Stilling. —Thence to the tactile area of the cerebral cortex.
NUCLEUS OF DEITERS (or external) and of BECHTEREW	Cerebellum. Fundamental tract of the lateral columns of the spinal cord.
SUPERIOR OLIVES	Anterior nucleus of the same side. Anterior nucleus of the opposite side. Internal nucleus of the same side. Nucleus of the roof of the same side. Oculo-motor and facial nuclei. Corpora quadrigemina. —Thence course towards the optic layer of the cerebral cortex.
INTERNAL GENICULATE BODY (receives the fibres of the anterior nucleus)	Temporal lobes. Reunited to that of the opposite side by the commissure of Gudden.

ferent but opposed ; it may, as has just been observed, continue its progress towards the cortex, but it may also return by paths which, for this reason, have been described as reflex. This retrograde course does not always and necessarily conduct the impulse to the muscles, but sometimes causes it to fall into nervous organs, where it finds an employment which is not clearly defined.

Held, who has studied the auditory (cochlear) nerve very thoroughly, divides the succession of its constituent elements into four distinct orders, which he calls systems. The *first order* is made up of those radicular fibres which proceed to the anterior acoustic nucleus and the acoustic tubercle, but certain of which also ascend in the superior olives, and some in the grey masses situated still higher. The fibres of the *second order* follow the same route as the preceding ones, either by starting from their strictly terminal arborizations, or from the collaterals along which they graduate in the nuclei, which they traverse without being totally exhausted therein. They arise then in the anterior nucleus and the acoustic tubercle, in the olivary bodies of the medulla oblongata, and in the trapezoid bodies, and in the nucleus of the lateral fillet ; some amongst the number go as far as the cortex (genuine fibres of projection of the second order) ; many pass

from one nucleus to another in a centripetal direction (inter-nuclear fibres of association); an important portion terminates in the corpora quadrigemina, and especially in the posterior; some of them become involved in the superior cerebellar peduncle.

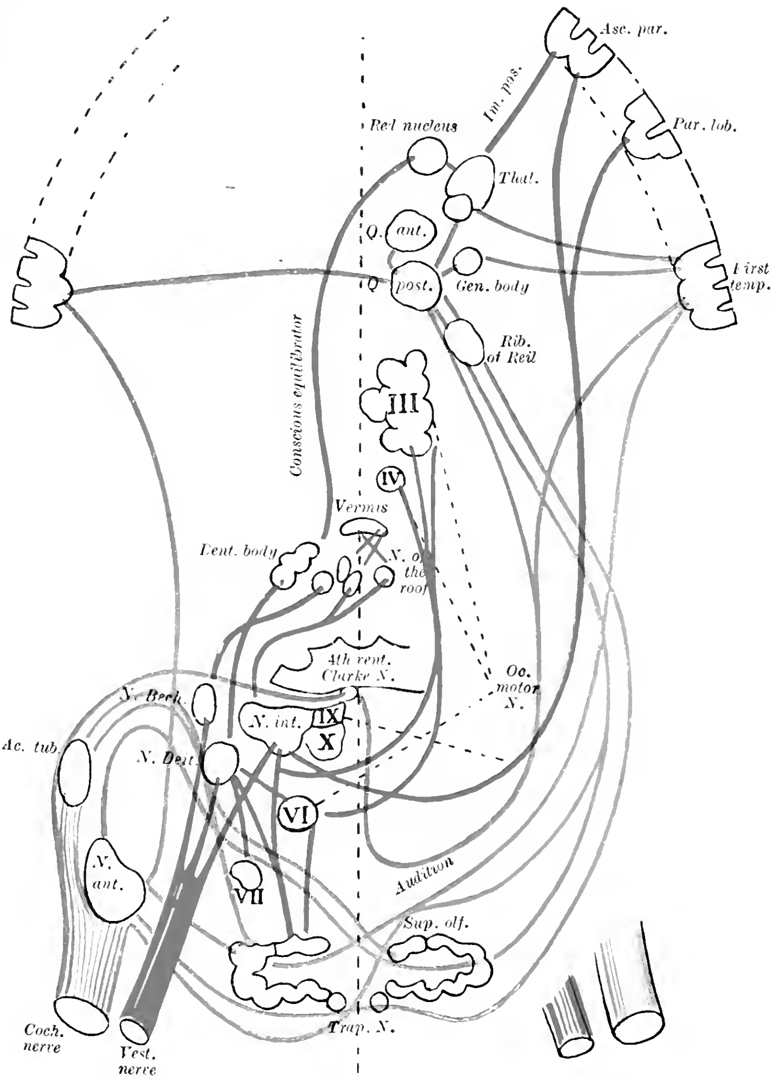


FIG. 249.—Diagrammatic representation of the auditory system; cochlear or auditory system properly so called in blue; vestibular system or that of orientation in red (copied from P. Bonnier).

III to X, nuclei of cranial pairs marked according to their conventional numbers.

The two other systems, that of the *third* and that of the *fourth order* are, with regard to the preceding ones, recurrent systems: they convey the impulse back in the direction of the periphery instead of involving it in the depth of the central masses. In the numbering of the systems having here as a basis the progress of

the impulse in the nervous cycle, the fibres of the third order will be found to be practically repeated, but with an orientation opposite to their conduction ; those of the second order follow Held's classification.[1] They redescend either from the cortex or from the corpora quadrigemina, and other deep nuclei, to the so-called primary nuclei of the auditory nerve, and, thanks to their different lengths, and also to the presence of collaterals given off on their progress, they are distributed in gradation over a certain number of these nuclei, but without going beyond the lowest amongst them. Amongst these fibres some must be included which form part of the *longitudinal bandelette* or posterior longitudinal bundle, whose origins are situated in the corpora quadrigemina and whose collaterals are distributed to the bulbar nuclei (oculo-motor) and whose terminals reach the anterior cornea of the spinal cord.

The fibres of the *fourth order* are motor elements arising from the bulbar nuclei (oculo-motor, facial) and superior medullary (nerves of the rotatory muscles of the head and the neck).

C. AUDITORY CORTICAL AREA

Cortical localization.—The sensorial area of *audition* is localized in *the posterior portion of the first temporal convolution.* Some authors consider that it also extends to the posterior part of the second temporal convolution.

Partial decussation.—*Each acoustic nerve is connected with the two auditory areas.* Complete deafness then (cortical) will only supervene when the convolutions above mentioned are destroyed on both sides. This arrangement obviously recalls that of the optic tracts as regards the retina. Yet nothing is known concerning the internal ear which recalls the mode of connexion of the optic nerve with the two right and left halves of the retina, and the laws regulating the distribution or the mixture in each cochlea of the auditory fibres in connexion with the two hemispheres are also unknown.

The localization of the sensorial auditory area in the temporal lobe is practically based on the same kind of proof as are the other analogous localizations, namely : loss of hearing, in the case of destruction (bilateral) of the above-mentioned cortical area [clinical observations in

[1] It may here be well to remember that the classifications of the different authors although based on the same anatomical and experimental facts, differ as regards the numbers given to the diverse orders or systems. All maintain, in principle, that there are four orders of *fibres of projection* which are divided on the one hand into two parallel groups, and on the other hand into two superposed groups according to the direction of the break which separates them. An imaginary surface passing through the periphery and the cerebral cortex is supposed to separate the sensory and motor, or centripetal and centrifugal, or afferent and efferent elements ; another imaginary surface passing through the grey axis is supposed to separate the neurons, the peripheral from the deep, and the inferior from the superior. Speaking generally, the peripheral or inferior neurons proceeding from the periphery to the grey axis, ór conversely, are called fibres of projection of the first order, and those going from the grey axis to the brain, or conversely, fibres of projection of the second order, whatever be the direction of the conduction. But other authors have inverted these numbers. If the impulse be followed in its cyclic progress, the classification of Held must be admitted. On the other hand, it must not be forgotten that, in addition to fibres of projection, there are a large number of fibres of association of all lengths.

man (Wernicke, Friedlander and Naunyn), experimental destruction in animals (Munck, Luciani and Sepilli]; atrophy of the system, as a result of its permanent loss of function; degeneration of its paths of conduction, as a result of the destruction of its origins or terminations; finally, embryological development of these paths, studied thanks to the more or less early myelination of certain bundles which this myelination renders more obvious in the midst of others.

The deep situation of the internal ear does not allow of the performance with the same facility of destructive operations comparable to the enucleation of the ball of the eye: nevertheless, section (unilateral or even bilateral) of the auditory nerve inside the skull can be performed.

On the other hand, the auditory paths may be attacked through the cortex. Destruction of the first temporal convolution brings about a secondary degeneration which may be followed into two distinct tracts, terminating in the internal geniculate body passing through the internal capsule, which they traverse perpendicularly to the general direction of its fibres. The internal geniculate body is itself degenerated; it has not been possible to follow the alteration further (Monakow).

These tracts are, in the infant of two months, myelinated before those surrounding them in the same locality; they may be seen starting from the internal geniculate body. to terminate (while becoming enlarged deep down and a little below the fissure of Sylvius) in two *transverse gyri*, which lose themselves in the first temporal; they are the portion of the corona radiata which belongs to the geniculate body, and attaches it to the cortex. The cochlear nerve is not myelinated till after birth; it is, amongst all the sensory nerves, the last to be myelinated (Flechsig).

In individuals affected with congenital deafness (deaf mutes), these convolutions have been found atrophied.

Physical deafness; psychical deafness.—An individual who, from any cause whatever, has lost singly but completely the apparatus receptive of sonorous stimuli is *deaf*. His deafness is of a *physical* nature. It abolishes for ever the physical conditions necessary for the production of auditory sensation. But he retains in his brain anterior auditory images; can invoke them at will, mutually associate them and represent to himself noises, sounds, words, phrases, and ideas corresponding to them. He is not psychically deaf, and he still regulates a great number of his actions, according to auditory representations arising in him by the association of auditory impulses which have reached him previously.

An individual who has singly but completely lost the posterior portion of the second temporal convolution, and also certain neighbouring regions (inferior operculum of the fissure of Sylvius, portion of the second temporal convolution) is not physically deaf; he continues to receive sonorous impressions and reacts to them by a great number of complex acts whose mechanism is instinctive or automatic, and especially of a defensive nature: but this individual is psychically deaf, and this psychical deafness allows of variations in severity, which also resemble those of the corresponding blindness, in cases of destruction of the occipital lobe.

a. *Cortical deafness.*—Should the cerebral cortex be attacked symmetrically in the aforesaid regions, the psychical deafness is total; there no longer exists, for this individual, distinct auditory sensation properly so called. At first sight he is not to be distinguished from an ordinary deaf person who has lost the power of hearing from disease of the ear, because in ordinary language the term audition merely designates the specific sensation of tonality, which is a cortical condition, and which he has lost for ever. But he has, nevertheless, retained reflexes of great importance; and the idea of space, which is of labyrinthine origin. and which is analysed in the sub-cortical systems, is preserved, since he has no vertigo.

b. *Deafness, properly called psychical.*—The lesion may be of such a nature that the sonorous sensation or that of tonality subsists in a distinct state, but it goes for nothing. The individual who perceives the sonorous sensation does not recognize it, that is to say, he does not recognize the *object* which has furnished him with the sensation. The sound of a clock no longer recalls to him the object clock. He is brought back by his lesion to the period of his earliest auditory education, with this aggravating circumstance: that he has lost the power he previously possessed of associating his sensations in time, either as regards their succession or their contemporaneous occurrence.

c. *Verbal deafness or that for words.*—A cortical lesion may have still more restricted consequences. It may allow of the subsistence of the sensation of sound and of recognition of the object, while suppressing the recognition of the *word*, that is to say, the appreciation of its conventional signification. The verbal sound "clock," will arouse no idea of the object clock. And this alteration itself is susceptible of degrees, since, in individuals speaking several languages, it may suppress one or several of these while allowing of the persistence of one, namely: that which was learnt first during childhood. In those who speak only one language, it may suppress separately a portion of it, such as the substantives, which are the proper names of objects.

Ideas of space; their relation to the cortex and the different senses

We owe to Ewald an experiment which shows the comparative part played by the labyrinth, the cerebral cortex, and the different senses in the conception of space and the preservation of equilibrium.

This experiment is made on the dog, and consists in effecting methodical ablations of the two labyrinths, and the two tactile areas, and in verifying after each operation the immediate effects and the permanent deficiency resulting from these ablations.

Suppression of the ideas of space of labyrinthine origin.—After complete ablation of one labyrinth, the animal displays disturbances both of audition and of the muscular movements. The first are permanent, the specific function cannot be replaced; the second ameliorate and seem to disappear at the expiration of a variable period of some weeks. The ablation of the second labyrinth brings about bilateral deafness, and completes and renews the disturbances of locomotion, which are reproduced with greater severity, but they in their turn improve, and after several months the animal will perform all its movements, whether instinctive, voluntary, or acquired, apparently with perfect precision.

Suppression of the ideas of space of tactile origin.—Afterwards the area called motor, but in reality tactile, of the cerebral cortex of one side is removed. The consecutive disturbances are those observed in an animal which has not undergone previous lesion of its auditory organs. The sensori-motor paralyses which result from this cortical lesion continue to ameliorate, and, though certain acquired movements may have disappeared, locomotion may at the end of some time be considered as entirely re-established. Then a fourth operation is performed, consisting in the ablation of the second cortical tactile area. Motor disturbances then appear which surpass in gravity all which it has been possible to observe after lesions of the portions of the nervous system governing movement. The dog can then neither jump nor run, nor walk, can neither hold itself upright, nor even lie down on the abdomen and the chest: it lies on one or the other side, and the most violent movements of its limbs no longer succeed in raising it.

Preservation of the ideas of space of visual origin.—But the movements of the head are preserved; it turns the head, and also the eyes, in the direction of the movements it desires to perform, or to look at the persons or objects which interest it. After some days it uses the head as a limb, and leans the muzzle on the ground, so as to make, with the help of the neck and trunk, an attempt to raise its body.

In this disorganized condition of its nervous system, the animal is still capable of a certain amount of re-education as regards locomotion; but, on one condition, viz.: that it is left in the *light*. Shut up in darkness, it remains quite incapable of standing up. And after this partial re-education, if light is wanting, the most simple automatic movements are difficult, if not impossible.

As the result of each of these four operations, the animal has lost one of the apparatus which furnish it with information regarding the position of its body and its limbs in relation to surrounding objects, and also as to its own segmentary attitudes. After the ablation of the two labyrinths, it lost the apparatus which furnished the most definite ideas of space, and those which are most frequently made use of, because they are rather of a reflex than a conscious order (sense of space of labyrinthine origin). After the ablation of the two tactile areas, it lost in addition the tactile and muscular sense (tactile sense of space). After the two first operations affecting the labyrinths, it succeeded in bringing about an apparently complete re-education of its movements of locomotion or otherwise, because

it still had at its disposition several senses, and more particularly the tactile sense. After the removal of its two tactile areas, it lost at the same time the labyrinthine sense of space, and the tactile sense of space. It is true that these two latter operations are not rigorously equivalent to the two former ones since, instead of abolishing the peripheral apparatus for the reception of tactile stimuli (which is impossible), a central apparatus has been suppressed, whose associations preside simultaneously over reflex acts like the former (but while allowing at the same time others to subsist in the subjacent ganglia) and psychical acts (which introduces a functional deficiency of a new character). But the disturbance of the sense of space has none the less been extreme, and has caused all the latent symptoms of the labyrinthine destruction to reappear.

After the loss of two senses out of five there still remains one available to the animal, the last which can provide it with information concerning the space surrounding it and to bring into operation the spatial sense : this is vision. Thus we see that it makes use of this sense to orientate its efforts and its movements, and to re-acquire, by means of a longer and more laborious education than the preceding, the power of standing up and of walking.

Part taken by the cerebellum.—It must be remarked that, however serious and extensive it may appear to be, the mutilation inflicted on the animal has still allowed of the subsistence in it of associations which are either important or essential for equilibration and co-ordination of movements. We have already said that the tactile sense, though very much compromised in certain respects, is not completely abolished as regards its relations with locomotion. Reflex associations continue between the sensory extremities (cutaneous, articular, and muscular) and the motor nerves through the cerebral ganglia and the grey medullary axis, and especially by means of that pre-eminently associating and co-ordinating organ, the cerebellum. On the other hand, the brain, from the psychical point of view, has only lost its tactile area, and has consequently preserved those conscious associations which act as a guide to the re-education of the nervous system.

The sense of sight is intact from a point of view which is as much psychical as reflex or automatic. The labyrinthine sense (specifically auditory and spatial) is out of court on account of its incapability of furnishing any impulse. The tactile sense (general and muscular sensibility) is psychically and reflectively incomplete, but partially subsists from a more specially automatic point of view. The central apparatus of motor association and co-ordination, the cerebellum, continues in its entirety, and again utilizes with the aim in view of locomotion and equilibrium, the ideas of space, at first discordant, which reach it from the subsisting sensory and sensorial areas.

Specific and common nature of functions : mechanism of the substitutions.—Not one of the suppressed apparatus can be considered as useless, and after the disappearance of each, it is not specifically and entirely replaced in the nervous functions. But, as the specific nature of each is only the result of a differentiation or an elaboration of the function common to all, it follows that substitutions are possible to a very great degree. These substitutions come into being the more speedily and effectively in proportion to the number of the subsisting specific organs, so that from this fact alone the possible combinations of association become more numerous. The cerebellum itself may be removed, provided that the brain and the senses are retained.

D. PATHS OF RETURN

Like all sensory and sensorial systems, the auditory system has its paths of return or of reflexion, which, either from the cortex or the subjacent ganglia, conduct the impulses to the exterior.

The motor organs on which the impulse is reflected, either from the cortex or the ganglia of the base of the brain, are the muscles of the external ear and the more deeply situated ones of the middle ear.

1. **Stimulation of the cortex.**—When this is effected in the temporal region in animals, *contraction of the muscles of the ear* is the effect produced by it ; this stimulation further reacts on the rotatory muscles of the head and the eyes to turn them in a determinate direction.

2. **Muscles of the concha.**—The muscles of the concha in man play an extremely restricted part and are nearly obliterated. In animals they answer the purpose of directing the auricular aperture in the direction required for collecting the sonorous waves, almost in the same manner as the oculo-motor muscles turn the visual axis in different directions. It is the facial nerve which provides the auricular muscles with their motor branches.

In order to proceed from the cortex to the motor nuclei of the bulb and the pons, the motor impulse follows fibres contained in the *external bundle of the crusta of the crus cerebri* (cortico-pontine path). Another portion of these fibres appears to rejoin these nuclei by a more devious path, which passes through the *optic thalamus*, whence in their turn they reach the grey bulbo-pontine matter. The first of these two motor paths is devoted to *voluntary movements*, the second to the movements of *emotional expression*, according to a division of attributes which appears to exist for all the senses and the motor combinations associated with them.

3. **Muscles of the middle ear.**—These have an equally precise function, but one of another order. The muscle of the malleus, by its contraction, renders the tympanic membrane tense, making it project into the tympanic cavity, and thus increases the intra-labyrinthine pressure. The muscle of the stapes, by its contraction, on the contrary, relaxes this membrane, and lowers the pressure in the labyrinth. The first of these muscles receives its motor fibres from the trigeminal : the second from the facial.

Further, vaso-motor reflexes (with bulbar centres) take part in maintaining (or in re-establishing after disturbance) the equilibrium of the tensions between the lymph of the internal ear and the air of the tympanic cavity.

The adapting and compensating mechanisms which take part, by reflex stimulation, in the exercise of audition and of orientation, will be examined in the study of the organs of the senses.

Functional analogy.—The analogy of function between the muscles of the auditory ossicles and the ciliary muscles of the eye is sufficiently great to have at once arrested the attention of observers. Obviously, these muscles obey solicitations of reflex order, which are controlled and regulated by auditory stimulation. It is probable that the reflex system to which they belong closely resembles in its arrangement that of the pupil, and that its centre of reflexion is situated in the region of the corpora quadrigemina ; but we possess no convincing experimental evidence in support of this inference.

CHAPTER IV

OLFACTORY AND GUSTATORY INNERVATIONS

LIGHT, sound, and the mechanical actions of bodies, which are the stimuli of our three principal senses, are *physically* known to us. We cannot say as much as concerns *smell* and *taste*, which for us are only sensations and have in themselves no scientifically defined objective character. Placed, the one at the entrance of the respiratory, and the other at that of the digestive paths, the senses of smell and taste give us information concerning certain qualities, either of the air we breathe, accompanied by odours, or of the food we introduce into the stomach after its preparation for swallowing in the mouth.

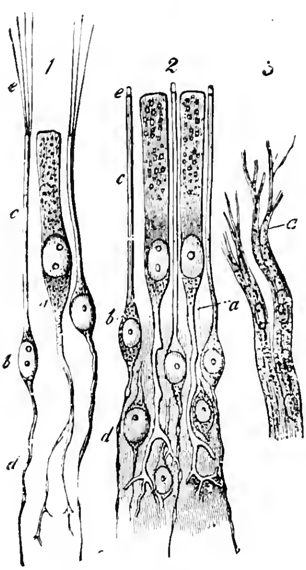


FIG. 250.—Elements of the olfactory epithelium.

In 1, elements in the frog; *a* epithelial cells of support; *b* olfactory cells with a deep prolongation (*d*) and a superficial prolongation (*c*), and with its terminal cilia (*e*).

In 2. Same elements in man, similar lettering.

In 3. Nerve fibres of the olfactory nerve in the dog, their terminal subdivisions in *a* (Frey).

At first sight it would seem that these senses serve as a means of preservation and immediate defence against the dangers which may threaten us through the paths of nutrition. This action of instinctive defence is, however, a restricted one; for very poisonous substances may be quite odourless and tasteless.

The olfactory and gustatory sensations in man do not possess an importance in any way comparable to that of the senses already considered, and the analysis, both objective and subjective, we can make of them, gives us less detail and allows of fewer points of view than as regards the other senses. It is reduced to a problem of localization, which is, however, but imperfectly solved.

A. OLFACTORY SYSTEM

At the present time it is principally from morphology that we must seek information concerning olfactory innervation. Experiment points out the pituitary mucous membrane

as being the seat of olfactory impressions, not, however, in its whole extent, but only in the superior portion of the nasal fossæ.

Field for the reception of impressions.—Special cells (*olfactory cells*) which are continuous with the fibres of the olfactory nerve, exist in this portion of the mucous membrane. These elements, intercalated between the epithelial cells of the mucous membrane, assume the form of elongated rods, ciliated on the mucous surface; they possess a nucleus by which they are increased in size, and a moniliform prolongation which attaches them to the olfactory fibres contained in the bundles which pass through the cribriform plate of the ethmoid bone. Thus they form neurons whose cells, located in the mucous membrane, have a ciliated receptive pole of very simple form, the axon of which terminates in the small rounded masses which are the glomeruli of the olfactory bulb. Such is the *peripheral*, or *inferior*, neuron of the system.

1. Bulbar portion of the system

Olfactory bulb.—Situated in the interior of the skull, the olfactory bulb is a *primary ganglion*, analogous to the bulbar nuclei of the auditory nerve, or to the grey columns of the spinal cord which receive the posterior roots, but by no means to the ganglia of Corti and Scarpa, or to the spinal ganglia, as has been sometimes held. The olfactory nerve (such as we must understand it) being made up merely of those fibres which, arising in the pituitary mucous membrane, traverse the cribriform plate in order to terminate in the olfactory bulb, its cells of origin retained in the mucous membrane, form there a sort of dissociated and spread-out ganglion, which is in all respects the equivalent of a spinal ganglion.

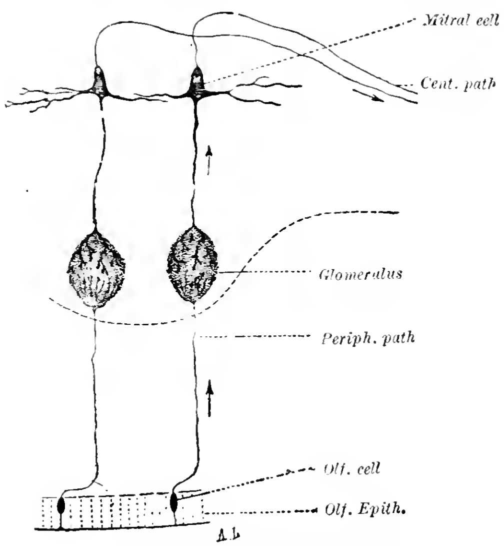


FIG. 251.—Olfactory paths.

Peripheral neuron (olfactory cell) and deep neuron (mitral cell).

Connexions of the terminal polar fields of the first and initial polar fields of the second in the glomerulus.

The olfactory bulb has the appearance of a mass of grey matter,

containing not only cells, but also polar arborizations of the same cells, by means of which they carry out their functional associations. It is a relay, a locality of association, and consequently of distribution and of transformation of the impulse.

Its organization.—Histological examination of this "centre" reveals in it details of great interest. The olfactory bulb contains the terminations of the olfactory fibres (those having their receptive pole and their cell of origin in the olfactory mucous membrane); it contains, on the other hand, special cells of different categories. The principal element is the *mitral* cell, so called on account of its resemblance to the mitre of a bishop. From the apex of this mitre an axon arises, which, following the olfactory tract, proceeds to the brain. Its borders and its base throw out protoplasmic prolongations (dendrites) which, taken as a whole, represent its receptive pole. These prolongations have different connexions, and it will be necessary to examine them separately. Finally, it contains the terminations of a variety of very singular elements, of which the other senses, and especially the optic nerve, furnish us with examples. It receives from the brain elements whose conduction is obviously centrifugal, which convey to it, through a purely sensorial organ, descending impulses of the nature of those furnished by the brain to the grey axis of the spinal cord, or by this latter to the motor organs of the periphery.

Connexions between the olfactory fibres and the mitral cells.—Those which are continuous with the base of the mitral cell descend, so to speak, in order to meet the terminations of the olfactory fibres. The connexions between these two orders of fibres, representing the opposite poles of two successive neurons, are effected in small masses isolated the one from the other, the *glomeruli* of the olfactory bulb. Nowhere can the connexions between the nervous elements transmitting the impulse be better seen than in these small masses, made up of *grey matter without cells.* The nerve cell (by this being implied the mass of primitive protoplasm which has remained more visible in the surroundings of the nucleus) is therefore not necessarily the portion of the neuron receiving the impulse. The function of the differentiated portions (the dendrites) is the collection of this impulse and its direction in the paths it must follow in the cell, by causing it to converge on the axon.

In an example of this nature everything is interesting, because under its simple form it supplies us with essential data concerning the organization of the nervous system. The glomerulus displays to us relations between the terminal and initial portions of two neurons placed in succession. It is generally maintained that this connexion is effected by contiguity, with interruption of the nervous matter properly so called. The mechanism, certainly of an extremely delicate nature, of the transmission of the impulse, at the present moment is completely unknown to us. The hypotheses which may be made on this subject need stand in no fear of contradiction, as they cannot be submitted to experimental investigation.

Numerical relations.—Though the functional nature of these connexions remains unknown to us, we may nevertheless observe, in the manner in which they are carried out, interesting details. In man, each olfactory cell is connected by a single axis-cylinder prolongation with a single mitral dendritic prolongation, ramified at the meeting-point of one with the other in the glomerulus, rarely with two of these prolongations. But there is not on this account either augmentation or reduction in the number of neurons placed in succession, this being exceptional in connexions of this nature.

In reptiles and batrachia, each mitral cell is provided with from two to five

dendritic prolongations which collect the impulse from an equal number of olfactory fibres into as many distinct glomeruli (P. Ramon).

In birds there are mitral cells which display as many as twenty dendritic or protoplasmic prolongations spreading out in as many glomeruli. Here obviously is a reduction in number of the neurons in the direction of the transmission of the impulse.

In the dog, the arrangement is the reverse ; when the olfactory fibre reaches a glomerulus, it there enters into connexion with five or six dendritic prolongations belonging to as many distinct mitral cells. Here we find augmentation of the number of neurons in the direction of the current of stimulation.

Functional varieties.—It is quite certain that these differences in the associations of the glomeruli correspond to functional varieties. In the inferior vertebrata, the parallel repetition of the olfactory cells and fibres corresponds to an enlargement in surface of the field of reception for olfactory impressions on the pituitary mucous membrane. In the dog and the osmatics, the multiplication of the mitral cells which, in the same glomerulus come into connexion with the same olfactory fibre, should correspond (like the augmentation of the cerebral olfactory system in these animals) to an elaboration of the sensation itself.

The osmatics, when compared with man and the primates, present a double increase in their olfactory power, namely : (1) through the absolutely larger number of their olfactory cells and fibres, corresponding to the extension of the sensorial area of the pituitary mucous membrane ; (2) through the relatively equally increased number of their mitral cells with regard to the first, this increase in number of the deep elements proceeding *pari passu* with a continually increasing complexity of their connexions both between themselves and with other elements.

Other connexions of the mitral cells.—By their angles the mitral cells give off other dendritic prolongations somewhat similar in shape to the preceding, but whose direction is different and which have no relation with the glomeruli and the olfactory fibres. These prolongations are on one side in contact with small cells having limited expansions, the *granules*, which, rare in fish and reptiles, begin to be numerous in birds, and still more so in mammals. Here may be seen cells of association mutually solidarizing or systematizing a certain number of mitral cells. The same lateral prolongations of the mitral cells come again into contact with the terminal arborizations of the elements of centrifugal conduction, which have been found to exist in the olfactory tract (Van Gehuchten) and convey an impulse of cerebral origin to the olfactory bulb.

The descending or centrifugal conduction of these elements is not a fact established by experiment, but may be affirmed (like that of the similar elements of the optic nerve) from the orientation of these elements in the olfactory tract, which orientation is exactly the contrary to that of the axons appertaining to the obviously sensorial or centripetal mitral cells.

The mitral cells, or at least the articulations of their lateral prolongations with the preceding elements, appear to be the seat of a reflexion of the impulse, effected in the opposite direction to the one we are acquainted with, and of which the grey matter, wherever existing, supplies so many examples.

If we recall what has been said above with regard to the numerous relations between the cells and olfactory fibres and the mitral cells, we shall see that, even in animals in which these relationships assume the most simple modality, without apparent reduction or increase of the number of the neurons in connexion, the impulse, in surmounting the ganglionic halting-place where these connexions come into being, finds new conditions, and enters into conflict with impulses of internal or external origin, which transform it from this moment by sending it forward and preparing it for other successive transformations.

Collaterals; pyramidal cells.—The axons of the mitral cells which direct the impulse towards the brain in localities which will be defined later on, have already partially allowed it to flow away in the olfactory tract by collaterals arranged in series throughout its length: these transmit it to fresh cells belonging to the grey matter of the tract (peduncle in animals): these cells, of small size and of *pyramidal* form, direct it anew by distinct paths towards the brain. Here again is another example of the arrangement, so often pointed out, of double paths, one direct and rapid (by fibres of projection to a great distance), the other indirect, slower and broken by relays (short paths of the grey matter), which present themselves, so to speak, to every impulse, diffuse and disseminate it, and so multiply its associations and its conflicts, that at last nothing of the initial form of the impulse is left subsisting in the surface receiving the impression.

2. Cerebral portion

The olfactory tract is connected with the brain by four roots: one, *external white*, which, after having crossed the fissure of Sylvius, is lost in the antero-external portion of the *hippocampal convolution*; one, *internal white*, which reaches the mesial surface of the cerebral hemisphere and is lost in the region known as that of the *olfactory commissure* towards the front of the convolution of the corpus callosum; a *grey* or *middle root*, which, plunging into the grey matter of the anterior perforated space, penetrates to a large extent into the head of the *corpus striatum* and joins the anterior white commissure of the brain. As regards the fibres involved in this commissure, they all cross to the opposite side; but some proceed to the opposite olfactory bulb, and others to the cerebral cortex of the opposite side. Finally, a *superior root* (also mingled with grey matter) is lost in the posterior portion of the two *orbital convolutions*.

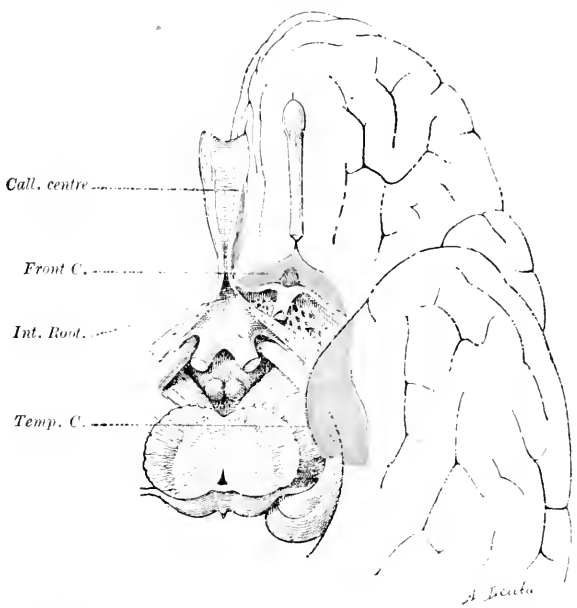


FIG. 252.—Cortical centres of olfaction (after Charpy).
The olfactory tract has been cut and its cerebral end turned backwards, in order to uncover a subjacent area of the grey matter appertaining to olfaction.

To sum up, these four roots terminate in a hippocampal region (external white root), in a callosal region (internal white root), in

an orbital region (superior root), and a temporal region (middle root).

a. *Hippocampal region.*—The olfactory area thus described corresponds more especially to the *crotchet* or *uncus* of the hippocampal convolution. Further, the *cornu ammonis* is included in it, and this connexion is effected, either by fibres which pass to this structure directly from the white external root, or by fibres which, proceeding from the white internal (or even the middle root), follow the devious course of the trigon to return finally to the *cornu ammonis.*

b. *Callosal region.*—This includes the olfactory chiasma, the point of union between the posterior extremity of the internal frontal with the convolution of the corpus callosum ; and, further, the adjacent portion of this last convolution (as far as the knee of the corpus callosum).

c. *Orbital region.*—This includes the posterior portion of the two orbital convolutions up to the cruciform furrow (in the human brain). In completely anosmatic animals like the dolphin, this posterior portion is quite smooth and atrophied, whence the name of *olfactory desert* given it by Broca.

d. *Temporal region.*—This region, in which are supposed to terminate those fibres which have traversed the median line in their progress to the cortex of the opposite hemisphere, is very little known, and is perhaps merely a prolongation of the hippocampal region.

Limbic convolution of the osmatics.—All sensory or sensorial systems have a cyclic arrangement, to which we have already directed attention. In the olfactory system, the general anatomical structure seems to display this externally, so that it becomes perfectly obvious. As Broca was the first to remark, this sensorial system, so important in certain species, is developed around the corpus callosum perpendicularly to the transverse direction of the fibres of this great commissure, and is represented by a convolution in the shape of a ring or limbus, the *limbic convolution*, lying on the mesial aspect of the cerebral hemisphere. Somewhat dissociated in man, in whom it is subdivided into two arched convolutions united by their anterior and posterior extremities, the one above the corpus callosum (convolution of the corpus callosum), the other below (hippocampal convolution), this convolution is distinctly continuous in the osmatics (animals with highly developed sense of smell : dog, otter, fox, etc.), to such a degree, indeed, that, starting from the olfactory lobe and peduncle by following its internal

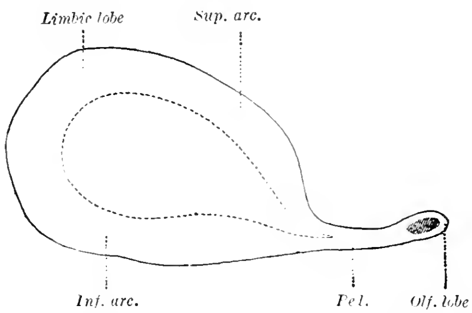


FIG. 253.—Diagram of the limbic lobe. In the form of a racket.

root, the boundaries of the whole corpus callosum will be traversed, of which the superior surface the splenium, and the inferior surface will be successively followed in order to regain the peduncle by its external root. Hence arises the comparison of this aggregation to a playing racket, of which the olfactory peduncle would be the handle and the convolution itself the enclosed network. This latter is completed by other circular formations which, either above or below the corpus callosum, form concentric circles of the same nature, and to which we shall return later on.

Osmatics ; anosmatics.—It is also to Broca that the distinction drawn between osmatic and anosmatic animals is due, these expressions being replaced by Turner by those of *macrosmatics, microsmatics* and *anosmatics* in order to indicate a graduation not sufficiently emphasized by the preceding epithets ; the dog is macrosmatic ; the dolphin is anosmatic ; man and the monkey are microsmatic. Such marked differences in the exercise of so important a function (the question here is of a sense taken in its entirety) should be rendered evident by inequalities in development of the nervous organs corresponding to it, and this is what anatomy and comparative physiology have demonstrated as regards the sense of smell. By taking as a guide the connexions by which to the external organ of smell (itself highly developed in osmatics) certain convolutions of the brain are attached, there will be found in them a development proportional to the function in each species under consideration.

Functional localization and balance.—The question regarded from this point of view reverts to that of the cerebral *localization* of the sense of smell, which comparative anatomy has undertaken to solve, failing definite clinical observations and experiments, these latter being too difficult to perform. This question is complicated by another which by no means diminishes its difficulties, namely, that of the *balance* of the special senses capable of mutual replacement in the directive function which devolves on one or the other, according to the particular evolution of the species, in the course of phylogenetic development. We have already pointed out a functional balance of another nature, between organs or systems, not juxtaposed, but superposed ; and it is thus that the brain in the superior vertebrata, in the primates and specially in man, monopolizes by centralization those federal associations which, in the inferior vertebrata, are organized in the cerebral ganglia or in the spinal cord, and in the invertebrata in the ganglionic chain. This centralization to the benefit of the brain does not operate without a differentiation of its parts and of its functions, and a kind of fresh metamerization, which is more or less marked at its surface, in

a new order. This corresponds to different senses, which have each chosen a special territory in the cortex.

The equivalence of these different sensorial systems does not imply their equality. In the progressive development of the brain, they are not seen to take an equal, or even proportional part ; but, on the contrary, the more or less rapid extension of one amongst them progresses *pari passu* with the partial regression of another. But as the general morphology of the brain does not sensibly alter in its larger features. or, to put it otherwise, as the functional associations of the elements are independent of the external form of the brain—the encroachment of the systems on each other may come about without leaving very obvious traces, and morphologically equivalent portions may be found to correspond to specifically differentiated functions, in the different animal species. Nevertheless, when the regression is very marked, or when, conversely, the development is exaggerated, more or less obvious morphological changes may be recognizable on the surface of the brain; and this is what stands prominently displayed in a comparison between the brains of the macrosmatics and the anosmatics, in spite of the difficulties arising from the want of definite boundaries between the different sensorial areas.

Indefinite boundaries ; mutual dependence of functionally differentiated portions.

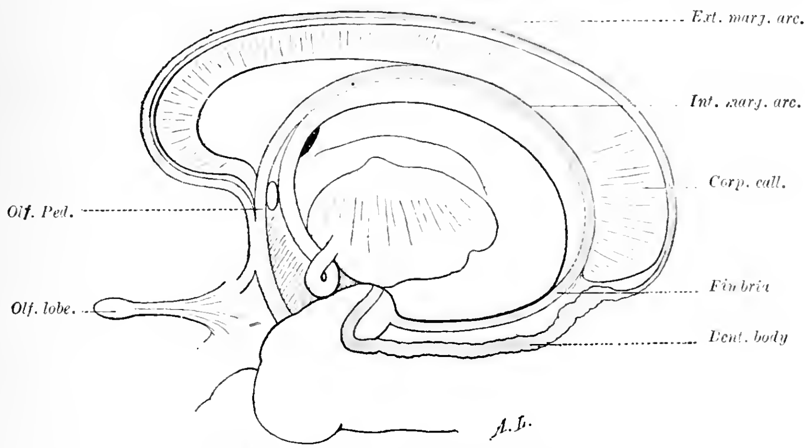


FIG. 254.—System of olfactory association.
Internal and external marginal arcs (diagrammatic. Charpy).

—It is important, however, to remember that, in the strict sense of the word, such limitations do not exist. If at the periphery of the body the sensorial areas are distinctly defined and without mutual connexions, this is not so at the surface of the brain which receives their fibres of projection. The areas for the reception of the impulses conveyed by the fibres of projection of each special sense are very distinct from each other, but are, in addition, mutually connected by fibres

of association, and these are more numerous than the elements of projection themselves. From this fact *it will be seen that there is no sense whose functional activity does not reverberate through the whole brain, and by it through the whole organism.*

The word *centre*, so often employed to describe these sensorial cortical territories, should be understood as implying *foci*, not only of *reflexion* on the spot by descending fibres of projection, but also, and principally, of *radiation* in the cerebral substance ; the brain being, like the spinal cord, but to a still greater extent, an elective organ of dispersion and distribution of the impulses reaching it by localized and specialized paths, it permits these impulses to flow away after multiplied transformations by functionally specialized and localized descending paths connected with the preceding and according to all possible combinations.

External and internal marginal arc.—The limbic convolution of Broca represents the ideally simplified scheme of the olfactory system. In reality this scheme is complicated by the adjunction of arched tracts of white fibres, more or less mingled with grey matter or interupted by ganglia, which reproduce its genera oval form, being, as they are, concentric to the limbic convolution (M. Duval, Schwalbe, Giacomini, Zukerkandl, Trolard, Bole). The olfactory system, to sum up, is formed of three concentric circles. The external one is the limbic convolution ; inside it is an *external marginal arc* comprehending the *fascia dentata* and the nerves of Lancisi, and which consequently passes above the corpus callosum. The third is an *internal marginal arc*, formed by the fimbria, the cerebral trigon, and the peduncle of the *septum lucidum*, and passes below the corpus callosum ; perforating fibres unite the second to the third arc, passing through the substance of this latter.

All these portions present tolerably natural mutual connexions. It is, however, impossible to say in what degree each is connected with the exercise of smell.

3. Evolution of the olfactory system and of its function

The evolution of the olfactory system in the zoological series forms an interesting chapter of comparative physiology. We will here endeavour to trace the principal data concerning it.

a. *Inferior vertebrata.*—In fishes, the cerebral cortex, strictly speaking, does not yet exist, being merely indicated by an epithelial layer not yet differentiated. In reptiles it is distinctly recognizable, and enters into communication with the olfactory lobe, though the other senses are not yet directly connected with it. " The brain of reptiles is an olfactory brain " (Edinger).

The sense of smell is not wanting in fishes ; it merely shares with the other senses the thalamus and the basal ganglia, which in these creatures represent the highest differentiation of the nervous system and of its functions. In reptiles, the new and exclusive relations of the olfactory bulb with the cerebral cortex allow of the subsistence of its older connexions indicated by two other tracts proceeding to the subcortical ganglia. One of these tracts reaches the ganglion habenulæ and from this ganglion a descending bundle arises, the activity of which is motor. The olfactory impulses are thus reflected in superposed stages of grey matter, viz. : the habenula, the *epistriatum* and finally the cortex, undergoing, in each case, a transformation of superior order which removes them from purely automatic acts.

The cortex of reptiles, of purely olfactory function, consequently corresponds to the cornu ammonis in mammals, and to their limbic lobe, in so far as it itself possesses olfactory function. Here also may be recognized a kind of fornix which is distributed between a genuine corpus mammillare and the ganglion habenulæ (Edinger).

b. *Superior Vertebrata.*—The olfactory system in man being taken as a basis of comparison, we see its different portions presenting a relative increase in the osmatics, and an equally relative atrophy in anosmatics, unequally distributed over the different arcs or convolutions of this system.

Macrosmatics.—On account of its antiquity (equally relative) in phylogenetic development, its convolutions are the first to be sketched in those species where the brain from being lissencephalic becomes gyrencephalic. At an early period a furrow separates the peduncle from the hippocampus, thus marking the extension in area of these portions. The convolution of the corpus callosum is also one of the first to be sketched in. Its bulb and its peduncle with their prolongations assume the proportions of a genuine lobe (olfactory lobe).

The roots of the peduncle are strong and the middle one occupies that quadrilateral space which, much diminished in thickness in man, ultimately becomes the anterior perforated spot ; it is this same root whose fibres decussate with

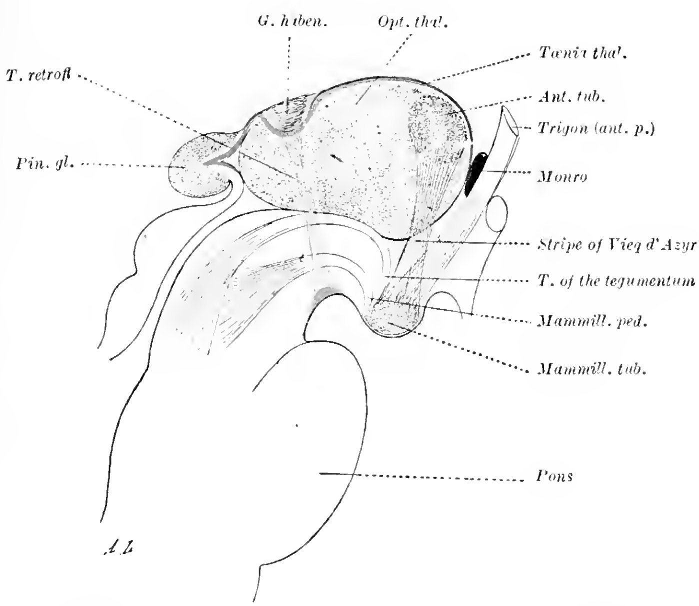


Fig. 255.—Habenular system (blue) and mammillary system.
Sagittal Section. Diagrammatic (Charpy).

those of the opposite side in the anterior commissure, and which further furnishes, according to Broca, an excito-reflex tract which by the peduncle rejoins the bulbo-medullary centres, whence arise the motor nerves. These roots connect the olfactory lobe to three regions of grey matter belonging to the frontal lobe above, to the hippocampal lobe externally, and to the lobe of the corpus callosum within. The organization of the internal arcs (external and internal marginal) is in proportion.

This is the arrangement in osmatics as a whole. Even in these animals, and in spite of their coherent appearance as a whole, we are not authorized to connect these different portions to the sense of olfaction in an invariable and strict manner.

Microsmatics.—In microsmatics, and especially in man, they have undergone an extremely marked reduction. This reduction is at the same time displayed

in the peripheral field of olfaction, by the more restricted dimensions of the pituitary cavity and the holes of the cribriform plate of the ethmoid, and in the deep portion of the system, starting from the olfactory bulb, whose peduncle is reduced to a tract and the roots diminished in proportion. The arrangement of the limbus is marked in front by the separation of the two superior and inferior arcs, and behind by a constriction in the shape of an isthmus which forms a connecting link between the convolution of the corpus callosum and the hippocampal convolution. Nevertheless, the limbic convolution persists in its general form. Olfaction seems to have taken refuge in the anterior portions (especially the hippocampal and that of the cornu ammonis) of the limbus, though we are not able to say what functions have replaced it in the remainder of its extent.

Relations and functions of the superior arc.—The relationships least well defined are those connecting the superior arc (convolution of the corpus callosum) with the exercise of olfaction.

The well developed root which in osmatics unites this convolution (internal root) to the peduncle, and the much frailer one (of the same name) which realizes the same connexion in man, do not allow of our doubting of the participation of the superior arc of the limbus in the perception of odours.

The augmentation in volume assumed by the anterior portion of this arc in osmatics seems definitely to settle this connexion by acquainting us with the fact that the posterior portion is connected with other functions. Conversely, the reduction in volume of this same anterior portion of the supra-callosal gyrus in primates (chimpanzee), proceeding *pari passu* with the reduction of the internal root and the relative maintenance of its posterior portion, confirms the same inference. In cetacea the regression terminates in the disappearance of the internal root; we should expect to find a parallel atrophy of the anterior part of the supra-callosal gyrus, but this does not appear to be the case. This anterior portion is the most developed, compared with the rest of the convolution; it is even traversed by furrows which increase its importance (Broca).

We may here observe a local appropriation by a nervous organ of functions which have not always been its own: but we are totally ignorant of the nature of these functions.

Olfactory commissure.—If the atrophy resulting in the cerebral cortex from the disappearance of the internal and superior root in cetacea is not indicated in the limbic lobe properly so called, it is nevertheless marked in a neighbouring region, the orbital area, by an effacement of folds and a smoothness of surface which forms the commissure of Broca.

4. Constitution of the olfactory system

The constitution of the olfactory system is, however, very difficult to unravel. As in other sensory systems, we may distinguish fibres of projection and fibres of association. Between the first and the second there is no essential difference. All the elements of the nervous system convey the impulse towards some new element which forwards it to its destination, through a series of progressive or regressive transformations. All equally associate other elements between themselves in a common function or one of aggregation. But the name of fibre of projection is more especially reserved for those passing over great distances and forming long paths, like those which directly unite the cortex of the brain to the grey matter of the spinal cord, and which connect localities where this transformation presents very different

values, in sometimes a descending and sometimes an ascending direction. The name of fibres of association is preferably given to those which unite in a transverse direction the fibres of projection, both ascending and descending, and which complete the reflex or psychical arcs which they constitute, by mutually associating in the brain its ganglia, or the grey axis of the medulla oblongata and of the spinal cord.

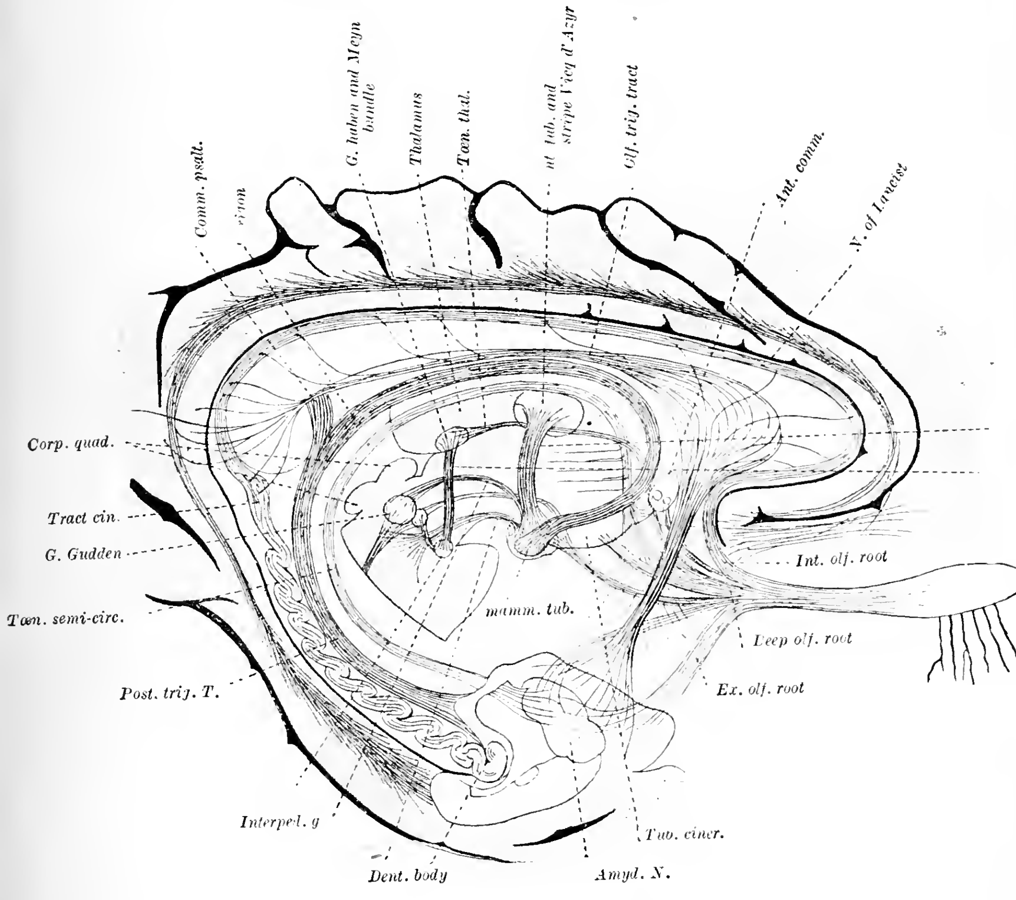


FIG. 256.—The olfactory system.
Olfactory radiations and cerebral trigon (after Dejerine).

In every case the two expressions have no signification exclusive the one of the other.

Inferior or peripheral neuron.—By analogy with the other specific systems we recognize in the olfactory system a first order of fibres, proceeding from the olfactory mucous membrane to the olfactory bulb through the cribriform plate of the ethmoid. This is the true *olfactory nerve* analogous to a posterior root, or, to put it better, an auditory nerve; it is formed of *peripheral* neurons, whose cells of origin have remained in the mucous membrane, and whose axon is spread

out in the glomeruli of the olfactory lobe. There, these neurons enter into communication with the dendrites of neurons of the *second order*, formed by the mitral cells whose axons are turned towards the brain, by following the olfactory tract (or olfactory peduncle) sometimes so incorrectly named the olfactory nerve.

Olfactory bulb, primary nucleus.—The olfactory bulb is the equivalent of the primary nuclei of the auditory nerve or of the retina of the optic nerve ; it therefore has the value of a primary nucleus. The *olfactory tract* which starts from it contains white fibres, which in their turn proceed towards the cerebral cortex : these white fibres are in part the axons of the mitral cells (true fibres of projection) and in part fibres arising from fresh cells disseminated along the tract, and which receive the impulse by collaterals given off by the axons of the mitral cells. We here find once more the overlapping of the polar fields, so often pointed out, which causes the impulse distributed by one neuron to reach several others, and most generally at unequal distances.

The most direct portion of the tract, that which answers to its fibres of projection properly so called, chiefly follows the external root, and by it goes to the anterior portion of the hippocampal convolution, and also to the cornu ammonis. Of moderate development in man (microsmatic), the cornu ammonis is rudimentary in the dolphin (anosmatic), and highly developed in the otter (macrosmatic). The *uncus* is not prominent except in those species in which this horn begins to retrograde. The tract is in strict developmental relationship with the *fascia dentata* or *corps godronne*, whose development it follows ; it is also connected with the grey matter of the *anterior perforated* or quadrilateral space of Broca, a layer much atrophied in man, but which is important in the osmatics and manifestly connected with the sense of smell.

We have mentioned above that the olfactory tract contains, like the optic nerve, descending or centrifugal fibres; fibres which in other terms bring back the impulse to its starting point in the olfactory bulb and to the contact of the mitral cells. This arrangement appears to ensure a true nervous circulation between the brain and the olfactory bulb, and reciprocally.

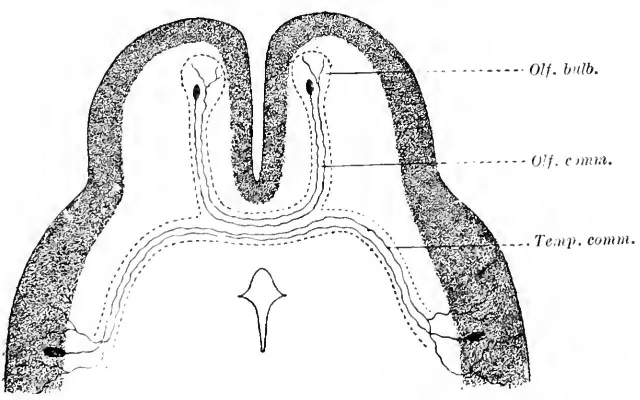


Fig. 257.—Arrangement of the anterior white commissure (diagram).

Olfactory chiasma, anterior cerebral commissure.—The fibres rising along the tract from its pyramidal cells, take part especially in the formation of the middle root and pass with it into the anterior commissure to reach the opposite side. They gain (at least in part) the olfactory bulb of the opposite side and form a commissure with an anterior concavity, distinct from another interhemispherical commissure with a posterior concavity, and equally distinct (according to some) from fibres decussated in the manner of an *olfactory chiasma* brought into being in this anterior commissure. By this path also the olfactory tract is connected with the optic thalamus.

The grey matter of the tract is an offshoot of that of the hemispheres, with

which it is continuous, and connected by fibres of association. The superior olfactory root is represented more especially by fibres of this nature proceeding to the orbital convolutions. But the most remarkable fibres of association of this system are formed by the trigon, the nerves of Lancisi and other formations of the same order.

Trigon.—The trigon is that double circular tract (one on each side, backed up by its congener and afterwards divergent) which, starting from the mammillary bodies, ascends by turning around the optic thalamus, redescends by pushing aside its posterior columns, and is continued by the fimbria which terminates in the cornu ammonis, whose relations with the olfactory bulb and its tract we have already noticed : the fimbria receives the fibres of the *fascia dentata* or *corps godronné*. The sensorial conduction is in reality effected in a direction converse to the above-mentioned course, and the impulses arrive at the mammillary body from the cornu ammonis ; the mammillary body possesses numerous paths for their distribution. Some of these paths pass through the crura cerebri, in the neighbourhood of the trochlear nucleus (dorsal ganglion of the roof of Gudden). Another of them, under the name of *stripe of Vicq d'Azyr*, ascends into the anterior nucleus of the optic thalamus. Thence a fresh connexion with the ganglion of the habenula, and from this by a tract called retro-reflex of Meynert, to the interpeduncular ganglion of Gudden, on leaving which we are in the external motor or centrifugal paths.

Psalterium.—In the interval between the posterior columns, the trigon shows fibres strung between the pillars like the strings of a lyre. This is an interammonian commissure formed by fibres of the fimbriæ of each side which decussate.

Olfactory tract of the cornu ammonis.—The trigon, in the anterior angle which it forms with the corpus callosum, leaves behind a tract which is detached from it, and of which a certain number of fibres skirt, in a scattered manner, the *septum lucidum*, pass in front of the white commissure, and crossing the olfactory roots, with which it has some connexion, contribute to form a *diagonal tract*, which terminates in the hippocampal convolution. It is from this tract that the perforating fibres are detached which rejoin the nerves of Lancisi through the corpus callosum.

Striæ of Lancisi.—The nerves of Lancisi turn externally round the corpus callosum, which separates them from the trigon and its olfactory tract. Starting from the *fascia dentata*, by the intermediary of the *fasciola cinerea*, they form a path of association of great length, which attaches these portions to the olfactory area.

Corona radiata, globus pallidus, and optic thalamus.—The olfactory convolutions (frontal and temporal) have practically the same general connexions as the other portions of the covering of the cortex of the hemispheres ; they give off or receive (or more probably, especially give off) fibres of the corona radiata. These fibres establish a fresh connexion between these convolutions and the *globus pallidus* of the lenticular nucleus, as well as with the thalamus.

Degenerations.—Gudden has applied his method to the study of this question. By shutting up a nostril in a new-born rabbit which was killed after some weeks, he established the fact of an arrest of development in the olfactory nerves of the bulb and of the tract. Destruction of the olfactory mucous membrane gave almost similar results. This signifies that destruction of the primary neuron involves as its consequence a certain amount of atrophy of the secondary neurons following it, from the fact of privation of excitations and want of functional exercise which is its result (atrophic degeneration).

If the olfactory lobe be injured, the destruction then affects the original cells of a certain number of deep cerebral neurons, whose axons degenerate as far as

their first relay, and at the same time atrophies may occur in the consecutive neurons. These degenerations, both direct and consecutive, have not yet been studied with the same detail as those of the other systems. Nevertheless, Treviranus had long ago noticed a certain degree of atrophy of the cornu ammonis as a result of lesions of the olfactory tract. The new methods confirm this observation, a degeneration may be observed in the cornu ammonis of the same side, and in the pyriform lobe, in the cornu ammonis, and in the olfactory bulb of the opposite side; thus this degeneration reaches both crossed and direct fibres. There is no degeneration of the root proceeding to the convolution of the corpus callosum (Loewenthal).

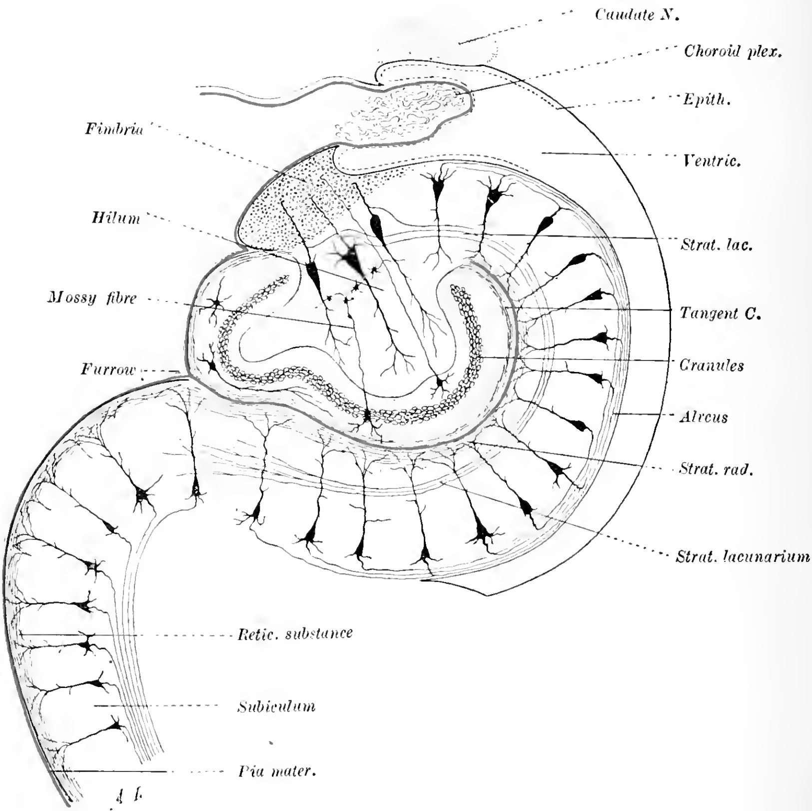


FIG. 258.—The cornu ammonis and the fascia dentata.

Transverse diagrammatic section; fascia dentata in blue; pia mater in red; only the fundamental elements are delineated; partly after Dejerine.

Absence of experimental and clinical data.—None of the cortical localizations is poorer in definite data (clinical and experimental) capable of checking the inductions of anatomy with regard to it. A case followed by autopsy has been observed, in which compression of the hippocampus by a neoplasm gave rise to attacks preceded by an aura consisting in sensations of very disagreeable odours. Besides being isolated, this fact by itself is hardly demonstrative. It is by the defi-

ciency in function that the sensorial localizations are easiest to establish, for functional exaggeration may be as well and even better explained by irritation at a distance than by an action directly localized on the cortical region under discussion. A double lesion affecting the cortical olfactory area would furnish the typical case required to settle the question, supposing that the anosmia had been verified during the life of the subject. Such a lesion must necessarily be very rare.

5. Olfactory motor paths

Motor activity is the external measure of sensibility. The senses being numerous, the most important amongst them will be the one having the most habitual relations with motricity, or, in other words, the one which is the most usual source of the informations by the help of which ideas are elaborated and acts determined. From this point of view it is easy to see how much the sense of smell has lost in us of the importance it possessed in the first vertebrata and still retains in some mammals. In the chase, which of old man was forced to follow to supply his needs, and which now (amongst civilized races) he only pursues for his pleasure, he is accompanied by the dog, on account of its osmatic aptitudes. From this example, it is easy to see the part played by olfaction in the representations which this animal makes for itself of the objects surrounding it. Its brain is furnished with olfactory images of an intensity and definite detail of which our own sense of olfaction may give us an idea, but of which our sense of audition, for example, is more or less the equivalent.

In man, the olfactory sense not only no longer directs the external motor activity, but now plays only a very incidental part therein, either with a defensive aim or for the search of the sensation itself. Also the motor activity directly connected with olfaction is itself reduced to some movements of the nostrils and of the thorax, co-ordinated in the acts of inspiration, expiration, or a more or less complete closing of the respiratory orifice. The facial, and with it the nerves of respiration, are thus associated to the olfactory nerve in a reflex action, which is, according to circumstances, defensive (constriction) or adapted to the exercise of smell (opening of the nostrils and inspiration).

Reflexes of adaptation.—In the most elaborated organs of the senses (eye, ear), in addition to the reasoned and voluntary movements which proceed from the activity of the senses, we may observe reflex movements of adaptation which are of three orders : (1) an external motricity of direction ; (2) an internal motricity of adaptation ; (3) vaso-motor and secretory activities which are equally necessary.

a. *External adaptation.*—In the *movement of the nostrils* (and that of the thorax) we observe, almost exactly, the action of the directing muscles of the eye or of the external ear. We do not know of any

internal muscle in the nostril having a function similar to the iris and the ciliary muscle, or to the muscles of the ossicles in the middle ear; but secretory epithelia regulate the state of humidity suitable for the impression of odours on the olfactory mucous membrane, and vaso-motor actions also regulate the circulation in this mucous membrane.

b. *Internal adaptation.*—As far as can be judged from what takes place at the entrance and the inferior portion of the nostril, the *vaso-motor and secretory* innervation of the organ of olfaction closely imitates that of the visual and auditory organs. The great sympathetic by means of fibres proceeding from the thoracic spinal cord, and by others which, originally contained in the trunk of the trigeminal converge with the preceding ones towards the spheno-palatine ganglion, balances the circulation of this region, moderates it by its constrictors, and exaggerates it by its dilators, which sometimes come from the cervical sympathetic, and sometimes from the trigeminal, and which are in both nerves very excitable in the dog. The system of the secretory nerves has probably the same topography and the same functional duality.

Relations to general sensibility.—We may repeat for the sense of olfaction what has already been remarked with regard to the other senses, concerning their relations with general sensibility. The olfactory mucous membrane, the peripheral organ of the sense of smell, possesses special nerves for odours: it also possesses others which here represent tactile sensibility, this latter having universally devolved upon the organs, is for this reason called general. The trigeminal ensures this general sensibility for the interior as well as the exterior of the nostril. Its paralysis (of functional or traumatic nature), hysteria, section of the nerve) causes, in addition to loss of general sensibility, a disturbance or even a paralysis of olfaction. These facts, clearly grasped by Magendie, would thus give rise to a belief in the direct participation of the trigeminal in the osmatic function.

Sensorial paralysis is here (as it is for sight and hearing) a secondary phenomenon. It does not immediately follow experimental section of the sensory nerve (trigeminal), but is the *consequence of the disturbances of nutrition* resulting from it. The explanation of these nutritive disturbances has often varied. The fact that they succeed the paralysis of an obviously sensory nerve causes them to be attributed to a disappearance of general sensibility, which would be the immediate and sufficient cause. We believe in the existence of centrifugal nerves governing the proper functions (and, by the medium of these, the nutrition) of the fixed elements of the mucous membrane, which elements degenerate as a result of section of their own nerves, as do all organs no longer receiving stimulation.

B. GUSTATORY SYSTEM

1. **Field of impressions.**—The field of gustatory impressions is limited to certain regions of the buccal mucous membrane; namely: (1) the base of the tongue behind the lingual V; (2) its tip and slightly also its borders; (3) the borders of the soft palate. These limits, however, may vary in individuals.

Papillæ of the tongue.—It is especially at the base of the tongue that the receptive organs of gustatory impressions have chiefly been studied. The mucous membrane is provided with papillæ of various forms (*filiform, fungiform, caliciform*). The organs of taste are buds disseminated on the fungiform and more especially on the caliciform papillæ, on the borders of the circumvallate fossa surrounding these papillæ, which would be better named *calicicoles*, since they arise in the interior of the calyx instead of forming it (M. Duval).

Taste buds.—The taste buds are small ovoid organs, whose long axis is directed perpendicularly to the surface of the mucous membrane. They appear to be striated on their surface, and these striæ correspond to elongated cells following the meridians parallel to the long axis.

Gustatory cells.—These cells are of two kinds : some are supporting elements ; others specifically differentiated elements, adapted to the reception of the gustatory impression (*gustatory cells*). The first exist on the whole circumference of the taste bud, and also in its interior. It is amongst them that the second are found ; their form is that of a nucleated element prolonged on one side by a ciliated rod which has an outlet outside the taste bud, and on the other by a thin fibre which is directed towards the deep surface of the mucous membrane. The gustatory taste bud is furnished with a kind of *pore*, situated in the superficial prolongation of its axis. By this pore the ciliated prolongations of the gustatory cells emerge, which are thus bathed in the buccal liquid containing sapid substances.

Equivalency.—The gustatory cells are not the equivalent of the olfactory cells ; they are not nervous elements. They are only in immediate contact with the arborizations of the nerves of taste, whose ganglionic cells are situated in the ganglion of Andersh as regards the glosso-pharyngeal. The initial extremities of these nerves penetrate into the taste buds by intrageminal fibrillæ and cover the gustatory cells with their arborization. They thus receive the exciting shock of the sapid substances at second hand, through the medium of the gustatory cells, just as the acoustic nerves, the nerves of touch, and the bipolar cells of the retina receive it from analogous cells.

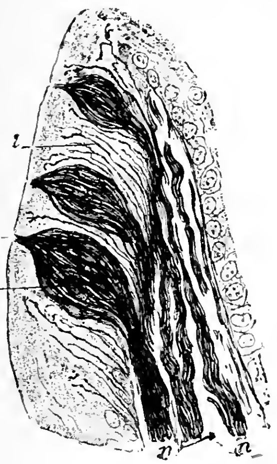


Fig. 259.—Foliated gustatory apparatus of the rabbit.

p, taste pore ; *s*, gustatory cells ; *i*, intra-epithelial nervous fibres ; *n*, afferent nerve of the taste bud (after Ranvier).

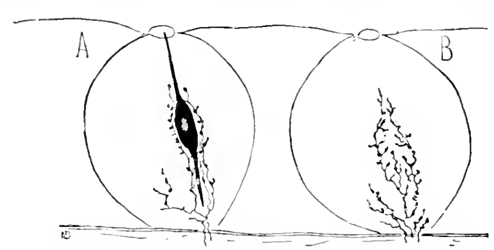


Fig. 260.—Receptive gustatory nervous arborizations.

A, taste bud with a gustatory cell surrounded by nerve ramifications ; B, the ramifications are alone indicated (after M. Duval).

Section of the glosso-pharyngeal nerve involves degeneration of the nervous

arborisations, and secondarily, disappearance of the gustatory cells, and atrophy of the taste buds (Ranvier).

2. **Nerves of taste.**—The base of the tongue has the *glosso-pharyngeal* for a sensorial nerve; the tip has, through the medium of the lingual, the *chorda tympani*, and the pillars of the palate have the filaments of the *palatine nerves*. These latter, and also the chorda, arise from the nerve of Wrisberg or small root (sensorial root) of the facial. The primary nucleus of the glosso-pharyngeal nerve and that of the nerve of Wrisberg approximate each other in the substance of the medulla oblongata (M. Duval).

Relations to general sensibility.—These are very visible and anatomically well marked in the gustatory apparatus. The area of gustatory impressions is sensible to those of touch and of temperature, and possesses tactile as well as gustatory nerves. These elements of different modes of sensation are mixed in the nerve trunks of the tongue and of the soft palate; the glosso-pharyngeal and the chorda tympani respond to mechanical excitation. In the glosso-pharyngeal the sensorial and sensory elements are mixed at starting from the origins of the nerve, though they are sorted out in the bulb into distinct nuclei; the elements of special sensibility proceed to the chorda by the nerve of Wrisberg; those of general sensibility appear to come to it from the trigeminal (perhaps by the petrosal nerves). Both of these being enlarged by centrifugal vaso-motor, and secretory elements which also pass by the nerve of Wrisberg, proceed to throw themselves into the trunk of the lingual (branch of the inferior maxillary nerve, itself a branch of the trigeminal) which bestows general sensibility on all the anterior portion of the tongue.

Secondary disturbances.—The dissociation of general gustatory sensibility is then only possible for the anterior portion, or tip, of the tongue, by cutting in an isolated manner the chorda tympani or the trigeminal in the skull. The resulting secondary disturbances of vascularization, secretion, and nutrition have often embarrassed the experimenters who have attempted to effect this dissociation. There are, however, facts sufficiently convincing to lead us to accept it in principle.

Unknown cortical localization.—With regard to the cortical localization of the sense of taste, we have no data, either observational or experimental; further, on this matter, morphological inductions are wanting. Neither the study of myelination nor any anatomical method furnishes us with any indications which are in the least probable as concerns the locality of the cortex which is connected with the nuclei of the glosso-pharyngeal nerve or that of Wrisberg. There is hesitation in connecting the gustatory area with the tactile region (as some do), or with the olfactory or an intermediate area (as do others).

3. **Reflexes of adaptation.**—As a set-off we are acquainted with reflexes of adaptation obviously appertaining to the exercise of the function of taste. The movements of the tongue are controlled by the hypoglossal nerve, whose nucleus adjoins that of the glosso-pharyngeal. Further, taste is connected with the act of mastication, of which act the motor nerves are also of bulbar origin. In addition to these strictly motor actions, taste, in a manner which is also reflex, involves vaso-motor and secretory modifications, the nervous mechanism of which is well known. It is contained in the great sympathetic and its bulbar dependencies. The vaso-constrictors ascend from the thoracic spinal cord through the cervical cord ; the dilators proceed to the lingual mucous membrane through the glosso-pharyngeal and the chorda tympani, to the soft palate through the palatine nerves ; these latter, and also those of the chorda tympani, arise from the nerve of Wrisberg. These vaso-dilatory elements are duplicated by secretory elements having the same origin, which, through the glosso-pharyngeal, proceed to the parotid gland, by the chorda tympani to the sub-maxillary and to the sub-lingual glands, and by the palatine nerves to the glands of the mucous membrane of the soft palate. The vaso-dilation proceeds *pari passu* with the secretion of the glands, and the two phenomena are favourable, indeed indispensable, to the exercise of the sense of taste, sapid impressions only arising in suitably vascularized and moistened mucous membrane. The sensorial impression excites, by reflex action, the phenomena of vascularization and of secretion, by the help of a cycle of adaptation, similar to that existing in all the other organs of the senses.

Painful reflex.—The secretion which is the most directly connected with the sense of taste appears to be that of the sub-maxillary and of the sub-lingual glands. The parotid secretion, more watery and abundant in certain animals (herbivora), seems to be especially connected with mastication (Cl. Bernard). The reflex secretion of the sub-maxillary gland may be easily provoked, by stimulating, in animals, the central end of the cut lingual nerve. Although the lingual contains gustatory fibres (coming to it through the chorda tympani), this secretion must not be considered as resulting from a stimlus of a purely sensorial nature reflected to the gland. The lingual, a branch of the trigeminal, contains chiefly elements of general sensibility, and the abundant flow of saliva following its centripetal stimulation is the expression of an ordinary reflex accompanied by pain. It is this reflex salivation which may be observed in dental neuralgia, or in other varieties of neuralgia of the trigeminal.

CHAPTER V

LANGUAGE AND IDEATION

LANGUAGE is a succession of motor acts which, by their combinations, usually express ideas.

A distinction is made between *articulated* and *spoken* language, which makes use of sounds (audible signs), and a written language, which employs letters (visible signs). Language is the great characteristic of humanity, and it forms the basis of civilized life. It is the *facultas signatrix* of Kant.

Emotional expressions.—Below the language of ideas, a *language of the emotions exists*. Every emotion is revealed by a series of motor acts which are both internal and external. The latter, which may be reduced to mere attitudes, reveal to others the passions which agitate us. Having a deeper root, this language is much more general than the preceding ; it is indeed both universal and natural ; animals comprehend it, and by its aid they communicate with each other and with us. Darwin has endeavoured to find in the structure of language a support for his theory of evolution. It is reasonable to suppose that the conventional language of the different human races is derived from the language expressive of the emotions, this being common both to man and to animals ; but it must be recognized that the traces of transition between one and the other are at present entirely lost or inappreciable.

A. FORMATION OF WORDS AND IDEAS

Language is expressed by *signs* which, being associated, form *words ;* words express *ideas ;* ideas arise in us from *sensations*, and sensations proceed from *impressions* made upon us by the external world. Such is the filiation of the phenomena. They are displayed in a nervous cycle of great complexity, and their mode of succession is naturally opposed to the above-mentioned filiation; that is to say, it proceeds from the impression to the motor act. We find, once again, in the function of speech that connexion between sensation and movement which underlies all nervous functions, and it is here presented under multiple forms ; we also observe in it both consciousness and unconsciousness, with their unequal and variable distribution. Most of the nervous mechanisms so far studied are displayed in it in a condensed condition. Further, it often fuses into a single act two, or even three, of the principal specific systems which share the cerebral

cortex between them. This function of language is pre-eminently adapted for furnishing a conception of the function of the brain as a whole.

1. Representations in consciousness

1. **Method of analysis.**—Language is one of the superior functions of the nervous system; on this account it is amenable to a double analysis, one purely *internal* or *subjective*, performed on ourselves, the other *objective* and *external;* conducted according to physiological methods.

Physical world and moral world.—For each of us there is an *external world*, opened out to us by our senses, and an *internal world*, which is more especially realized when we close the senses to impressions from without. The first is the *physical* world, the second the *psychical* or *moral* world. The first is formed of objects and phenomena which we discern by our senses, but *indirectly*, inasmuch as it is external to us; the second is formed of moral representations or phenomena; and this we comprehend *directly*, because it is internal to us.

The physical and psychical worlds are, by their nature, incapable of reduction to a common element. Every attempt to bring them back to a unity which may probably exist at the foundation of things, but for the perception of which our position is unfavourable, fails before the arguments of evidence and of common sense. Nevertheless, we feel the strict connexion and dependence in which they exist with regard to each other. Further, between the operations performed within us on representations, and those effected external to us on objects and movements, we detect an analogy which ordinary language sanctions by expressing them in similar terms. Internally, as well as externally, to ourselves, we recognize amplifications and reductions, separations and reunions, concordances and oppositions, actions and reactions, etc.

Internal and external observation.—When we carry out an analysis of this nature, on the one hand in our own consciousness, and on the other hand with regard to the brain of a fellow creature considered as an external object, we apply the two methods to the study of a question fundamentally one and indivisible regarded from two opposite aspects, and each method is almost useless alone. Consciously or unconsciously, we call upon them to lend each other a mutual support. It is not difficult to discover that the two analyses thus conducted, the one in the moral and the other in the physical world, though they may not be far advanced as regards actual results, are not superposed in the things with which they are concerned. The method by which we

take cognizance, with our senses, of objects external to ourselves is more particularly an analytical one. It furnishes us as concerns the brain of a fellow creature (and, therefore, also our own) with details which our internal vision can in no way grasp. Concerning the *static* organization of the elements it has thus discovered, it possesses and continually acquires data which are not without importance, but which will really bear fruit only when the day arrives in which it will see this dead matter in a state of movement and can then comprehend the incessant modifications which constitute its *dynamic* state.

Our internal sense also discerns representations ; but, amongst these representations, precisely those of the material objects (brain and its component elements) presiding over its activity and its existence are effaced. The simplest of these representations (the sensations), those which enter as elements into the psychical aggregations which minister to the operations of the mind, those beneath which the internal sense no longer analyses or distinguishes anything, are physically brought about by a physiological complexus of a very elevated organization (cerebral cortex), of which it can grasp neither the elements nor the limits. The play of the nervous forces, on which it depends, while at the same time directing it, eludes it in the same way as do all material objects and phenomena. Should this play of forces, however, become accessible to it, it will be so by means of a detour ; that is to say, by passing once more through the external senses, which will then provide it with its representation and nothing but its representation.

Thus it is necessary for us to watch over ourselves alternately with our eyes, with our reason. We are acquainted with the fact that the two analyses, although following parallel paths, do not overlap each other. We shall rarely call upon them to verify each other. We rather, by taking each in its own sphere of action, seek to complete one by the other.

2. **Multiple operations of the mind.**—Internal observation shows us a distinct series of operations in ourselves, to which ordinary language has given different names.

Sensation, knowledge, recognition (psychological), *representation, memory, attention, idea, will*, are all internal phenomena (eluding the external senses) which every one can distinguish from each other, and the relations and connexions of which we are able to recognize.

Primordial element, sensation.—Of all these phenomena, sensation is the most elementary. This is the original fact whence all others are derived by extensions, associations, dissociations or different combinations. In itself it is simpler than it appears to be. A sensation may be isolated from every other to such a degree as to leave no

trace behind it. The sensations revealed by the cries of an individual under the influence of chloroform, and which, on awakening from this influence, he forgets, are of this nature ; those which first penetrate into the nervous system of the new-born child are of the same order ; they are independent elements, not united between themselves. We must not forget that sensation is a physiological complexus ; it requires for its development a highly elaborated system of neurons which receive at its origin an impression from the external world ; but, for our internal sense, sensation is pre-eminently the psychical element.

Its residuum.—An impression, by being itself renewed and by renewing the sensation, forms habitual paths for itself in the nervous system. *Not only does it create its own paths, which cause it to have in this system always the same reverberation, but it continues permanently in them.* All sensation leaves behind it what is known as a *residuum.* I, for my part, consider that this permanence has for its physical condition a circulation of the impulse in the interior of closed cycles, which renew it automatically in an indefinite manner.

Strong and weak state.—The impression, attacking at the periphery a system which has already been subjected to anterior impressions, would then be no longer in the condition of an impression which was the first to fall into this system. It becomes associated with the residues left by antecedent impressions ; it is continuous with the latter in time. From the *weak condition* into which they had fallen, it brings them back once more to a *strong condition.* It synthetizes and identifies itself with them. And hence it follows that we are not, so to say, conscious (except by an artifice of reasoning) of a simple sensation, but only of one which is prolonged or renewed.

Memory.—This phenomenon of synthesis in time is called memory. Forasmuch as it identifies a freshly produced sensation with one previously experienced, it is *recollection.* Forasmuch as it enlightens us with regard to the original cause of the impression and sensation, it is *knowledge.* And forasmuch as it associates together all this knowledge of different forms, and derived from varied sources, according to a logical classification, it is acquired *experience.* All these data of internal observation are self-evident.

Consciousness.—They are self-evident because they are illuminated by that internal radiance which we call *consciousness :* with the exception of residual sensation, which escapes it. In the time which separates the first or anterior from the renewed sensation, there is a passing over from consciousness to unconsciousness ; then, when the renewal takes place, a converse passage from unconsciousness to consciousness. Consciousness is susceptible of degree, and its variations and gradations

are infinite; these gradations we may observe in ourselves, until it reaches that threshold below which it practically disappears. On the other hand, physiological facts prove that, when sensation is no longer obvious to us, it yet survives in its physical conditions. The conscious and the unconscious reflex arcs are formed in the image the one of the other.

Forms of sensation.—Like the systems presiding over them, sensations are of different modalities (sight, hearing, touch, etc.). The combinations of the impressions from which they arise are also different: this is what is called the *form* of the sensation. By dint of being repeated in us, as the result of similar impressions, the sensations assume a signification, a determinate symbolism; this is what is called, in the language of the schools, the *content* of the sensation. The content is the *object*, the thing in harmony with the sensation.

Representations; psychical images.—By these mechanisms, some connecting sensations in time and others simultaneously demonstrating to us the varied qualities of objects, a *representation* of the external world is established in us: this is the aggregation of our *psychical images*. These images are classed, arranged, systematized in the unconscious, and they may be evoked at each impression of the object to which they correspond; that is to say, at each sensation recalled by it.

3. Analysis and synthesis; formation of the images of objects.—Each sense, each sensation, enables us to know and to recognize only one quality of the objects which have made an impression on it. The mind, the cerebral activity, and the thoughts are employed in separating and abstracting the similar qualities of different objects, and attaching them to the object which possesses them all together. By this new operation of the mind, recognition of the sensations leads to recognition of the objects. To refer once more to Charcot's example, so often quoted, a clock may be heard, seen and touched. The mind connects so intimately the forms of the three sensations reaching it from the object "clock," that, at each new impression proceeding from this object to one of the three senses (vision, hearing or touch), the latter is at once recognized. One impression alone is sufficient to give rise to the *three* sensations, one impression being very strongly and the two others but feebly marked; the idea of the object springs from this association.

This is thought in its most lowly aspect, and in this form it appertains both to man and to animals. By means of its associated sensations, the animal elaborates ideas which, presenting the most elementary degree of generality, are capable of so directing its acts as

to ensure self-preservation. In this way a foundation of *concrete ideas* is effected.

Thought, abstraction.—But "thought" in the ordinary sense of the word, implies a process of separation and re-composition, or, properly speaking, of *abstraction*, which is carried much farther, and in a great degree distinguishes human thought from that of animals. The animal, as we have just said, thinks by means of its sensations; man thinks with abstract ideas, that is to say, with words. By a new process of internal analysis working on psychical images, he elaborates a collection of *verbal images* whose symbolism is far more exalted than is that formed by his images of objects. This is language heard and spoken, to which civilized man adds language read and written.

Formation of verbal images.—To return to the preceding example. The word *clock* when first heard by the child does not awaken in him the image of the object "clock," nor, indeed, that of any known object; at first it only tends to create, and in fact creates, a new auditory image, neither more nor less important than those he already possesses. But this auditory image, if evoked in determinate and suitably chosen circumstances, gives rise in him to a new process of abstraction, carried much farther than the preceding, by means of which it acquires a symbolical value of a truly general order. The instinctive operation by means of which the child's brain acquires this new faculty is one of the same nature as those taking part in the reasoning faculty, such as it is methodically exercised, according to logical laws, in the adult.

Reason is the faculty possessed by the human mind of performing such operations. Further, it is by the superposition, no longer simply of psychical images, but of concrete ideas formed by the superposition of these images, that the mind, proceeding from abstraction to abstraction, at last attains to the acquirement of general ideas, *abstract conceptions*, properly so called.

Comparison.—Comparison always arises from a superposition of two things, having points of resemblance in common; and, again, this process of superposition emphasizes the features displayed in common and eliminates those of difference. All comparison is an *internal experiment of identification* of sensations and ideas; this experiment being followed or not by an anticipated result, but in either case having its own significance. The immense advantage possessed by the superior animals over their inferior brethren, and of man over animals, is that, by means of sensations and ideas, they can perform those experiments which the uncultivated or irrational creature is forced to bring about by the help of its motor powers. From this results an enormous economy of time and strength.

Thus the infant accumulates a collection of verbal auditory images. By means of a fundamentally similar mechanism there will be formed later on a collection of *verbal visual* images. The process by which the latter are acquired is more obviously analytical merely because the capabilities of the subject are then more developed, and, the faculty of spoken language being acquired, this aids in the acquisition of the written language.

2. Motor actions of written and spoken language

In spoken or written language the complement of the sensorial or intellectual operations is represented by motor acts, and these enable us to reproduce externally those audible or visible signs which have made an impression on our own senses, so that they may make a similar impression on the senses of our fellow creatures. It is this exchange of symbolical signs, rendering feasible an exchange of ideas, which places the function of language in the highest rank amongst the functions which are described as those of external relation. As in all the functional systems, *the development of the sensory or sensorial precedes that of the corresponding motor aptitude.* The articulation of sounds in the child follows more or less closely on the acquisition of either simple or verbal auditory images ; further, from the very first moment in which it becomes possible for it to do so, it aids and singularly accelerates this acquisition. Writing also follows reading, so soon as the child acquires the first rudiments of the art. The motor acts of written language are, however, when required, at the service of auditory images, and articulated speech may also aid in the interpretation of the visual images of written language. It is possible to answer a verbal question in writing, and also possible to reply to a written question verbally.

Spoken language possesses the advantages of facility and promptitude ; it serves for the everyday exchange of ideas. Written language is more artificial ; the pen and the book are factitious organs interposed between those conversing ; but it has the advantage of the permanence of the written signs and of the possibility of multiplying them indefinitely by printing ; it also points to an essential progress in human culture.

Deaf-mutism.—In those deaf from birth speech also is wanting ; this is the result, not of a motor paralysis of the organs of phonation, but of the absence of auditory sensations. It is to the imitation of spoken language that the child directs his first efforts, with the object in view of emitting sounds similar to those he hears ; his own ear instructs him concerning the success of his attempts, and at every moment corrects his faults of articulation. In those born deaf, the auditory sensation being congenitally absent, articulate speech becomes impossible. This is a fresh example of the close link which connects movement and sensation amongst the varied forms of both.

Thus visual images in the deaf-mute assume a preponderating importance. Further, so that any one afflicted in this manner need not always be obliged to write his thoughts, a language of rapid manual signs which replaces articulated speech has been invented.

Functional compensation, tactile images.—In the blind visual images are entirely wanting, and in them blindness may be compensated by the sense of touch, on which practice will confer a greater acuteness. The blind can read by touch books with raised lettering.

The case of Laura Bridgeman is a remarkable one. Becoming blind and deaf at the age of two years, this child had nothing left to fall back upon but the sense of touch, and she remained uneducated up to the age of seven years. Doctor Howe, by the aid of signs stamped in relief, provided for her a *tactile speech* by which she could form *verbal graphic images*, and could thus enter into intellectual relationship with those surrounding her. Intelligence, until then arrested in its development, suddenly took possession of its inheritance.

Part played by the muscular sense.—The sense of hearing takes part in spoken language, the sense of sight in written language, and the sense of touch may artificially supplement either or both of these senses. It must be observed that the muscular sense, which is another variety of that of touch, continuously aids the motor phenomena by which speech and writing are performed. It takes part, it is true, in a secondary manner ; nevertheless, its activity is an important one. Speech, in fact, is not dependent upon the ear alone in order to yield a suitable articulation of sounds ; neither is writing exclusively dependent upon sight for the co-ordination of the movements of the hand. If absolutely necessary, it is possible to write with the eyes closed ; those who become accidentally deaf yet preserve the power of articulation and the intonations of speech. Thus the sensation which guides and regulates the muscular movements is entirely muscular and tactile.

We may then, even in individuals in possession of all their faculties, admit the existence of motor images (both of articulation and of writing) ; only those images are unconscious ones. In deaf-mutes, motor representations of gestures acquire an exceptional importance, and it is probable that they perform mental operations by means of these representations, just as we ourselves with auditory or visual images.

In those attacked by verbal blindness, who have thus lost the faculty of reading, the performance with the right hand of the movements necessary for copying a word will sometimes re-awaken its symbolical signification.

Remark.—Before being able to speak, the child must possess some auditory verbal images ; and before being able to write, he has already acquired some visual verbal images. His education in speaking and writing has the effect of creating phonetic and graphic motor images in him. The latter consist in associations of elements called centrifugal or motor, as do the former in those of centripetal or sensory elements. We may here point out that neither the mutual association of centripetal elements, nor that of centrifugal elements by itself, alone constitutes systems whose function is isolated, but that each of the two, taken individually, is initially completed by the adjunction of fibres of opposite conductivity, so as to form cyclic systems which alone are capable of action. In fact impulses reaching the auditory nerve are quickly reflected to the motor nerves of the adaptive apparatus of the ear, and those which reach the optic nerve are in the same way reflected to the adaptive apparatus of the eye ; thus are constituted the systems which we call sensorial, merely, however, on account of the importance taken therein by the phenomena of sensation in relation to movement, but which, in fact, are sensori-motor.

The system which we call motor (phonetic or graphic) is not entirely free from

sensory elements. By a kind of converse reflexion, the impulse which has descended into the muscle leaves it to ascend towards the brain by the nerves of the muscular sense. Motor, like sensorial, images are practically aggregations in which either motricity or sensibility are associated in unequal proportions. By their mutual association in the exercise of the function of spoken or written language, these sensorial and motor systems describe an arc with a larger extension, indicating the general course of the impulse, but which is complicated by a certain number of partial internal cycles which must be taken into account in the analysis of the general mechanism.

Voluntary determination.—Thus, by association of sensations in time, by their diverse forms and the mutual comparison of these forms, by the representations arising from this, by the formation of images, by the organization of the latter, first into concrete, later into abstract ideas, and by the methodical classification of these data in the mind, a store of personal experiences is laid up, which goes on increasing in proportion to the number of new sensations added to the preceding and to the continuance of the process of organization to which they are submitted. This store is greater than we ourselves imagine. Consciousness only partially illuminates it, and usually does so on the arrival of a new sensation evoking the series of psychical acts which are in harmony with it. Mechanisms habitually unconscious aid in abbreviating these operations. Their automatism suppresses deliberation, which would involve delay. Deliberation has no influence except as regards the function of direction, which is alone enlightened by consciousness. It is this deliberation which causes the voluntary act. It is this which determines the answer, delays or precipitates it, and dictates its meaning, according to motives which have been more or less carefully estimated and compared.

Automatic language.—The most deliberate premeditated speech allows in its performance of the intervention of numerous and complicated automatisms. It may even become entirely automatic, as sometimes happens in a reading or recitation delivered without regard being paid to the sense of the words. In this case impulses reach the muscles in a predetermined order, of which the brain alters nothing, resembling, in a sense, the more or less complicated electrical waves which, in a telephone, proceed from the manipulating to the receptive apparatus. The reflex arc of automatic speech may connect: (1) vision with phonation (automatic reading); (2) hearing with phonation (echo of speech); (3) vision with writing (copying); (4) hearing with writing (dictation).

In these examples, language becomes reflex, that is to say, unconscious, without ceasing to be cerebral. Conversely, it may remain conscious and have no external motor effect. Language, in fact, has the very closest connexion with thought, and thought is a continuous phenomenon. Man expresses his thought in speech, but he first thinks that which his speech expresses.

3. Internal language

We possess an internal language similar to external language, the

only difference being that the former is heard by ourselves alone. This language is *spoken only* in the sense that it is present in our consciousness under the form of sonorous images of which the rhythm, tone, intonations and inflexions are habitual to us, and not under the form of the visible signs of writing, or other analogous symbols. An exception must be made in the case of deaf-mutes, who are unacquainted with the audible signs of language, and who make use for internal language of the same signs as those employed for their external language.

Internal speech is so similar to external speech that it is possible to pass insensibly from one to the other; a *loud, low, internal* voice and *whispering* are merely various degrees of the same phenomenon. The essential difference does not, indeed, arise from the relative intensity of the vocal motor act, but from the fact that, in internal speech, we have no other auditor or interlocutor but ourselves. Our own speech, whether loud or low, has on our own hearing and on that of others, the effect of a sensorial excitation, evoking ideas, suggesting answers, and so on, in a series of motor sensitivo-motor cycles which engender and succeed each other in us just as occurs in a well-arranged train of thought (Egger).

The relations of the idea to the word, and of the word to the idea, are the same both in internal and external speech, because the order and succession of the phenomena are precisely similar in both. Internal, like external, speech is *automatic* (as is often the case in mental prayer) or well thought out (as when a lecture is prepared).

Internal resonance.—How is it possible for our own voice to resound internally in us when, apparently, no auditory impulse ascends to the brain? Whence comes the impression which simulates a word whispered in our ear which has no real existence? In loud speech the circulation of the impulses is continuous; the brain stimulates the muscles of phonation, which, by causing the air to vibrate, in their turn stimulate the brain. Thus the brain retains the echo of its own excitations, which are returned to it in the order in which it sent them itself to the muscles of phonation. In internal speech, the cycle seems to be absolutely broken in its inferior portion and is really so between the larynx and the ear, but it is nevertheless completed by other paths. The air no longer vibrates, but the muscles are not absolutely motionless.

Motor tendency.—In internal speech, self-observation will prove the occurrence of very slight movements of the tongue and lips, and this to some extent tends to demonstrate the motor quality of internal language. These movements (incapable of causing vibration of the air) have a sensory echo in the nervous system, inasmuch as we are conscious of them. The cinæsthetic sensations elicited by them (muscular sense) give rise by associations to corresponding auditory sensations. Internal speech, which is audible only to ourselves, would thus be an instance of tactile motor images which are perceived as auditory images. Whatever may be its explanation, the fact of the existence in internal speech of an attenuated motricity is undeniable: every sensory impression is

made manifest by movement or tendency to movement. Suspension, adjournment, arrest of the motor phenomenon is the appanage of well considered, deliberate, and voluntary acts, just as is its immediate performance that of reflex, unconscious and involuntary actions.

Another explanation.—The circulation of the impulses in internal speech may be explained in yet another manner. The impulse which descends from the brain to the grey nuclei of the inferior system for the performance of movements may here, perhaps, undergo a reflexion in the opposite direction which may cause it to re-ascend to the brain, thus saving itself the journey which, in articulated speech, it would be forced to make from the motor nuclei to the muscles, and thence to the sensory bulbo-medullary nuclei which would forward it once again to the brain. Instead of receiving at third hand an impulse which has successively passed through the nuclei and motor nerves, through the muscles and, finally, through the nerves of muscular sensibility, the sensory bulbar nuclei receive, directly from the brain, an impulse having the form of the movement which it is intended to accomplish, and they send it once more to the brain to announce the no-longer muscular, but entirely nervous performance of the act controlled by it. In this intra-nervous circulation, the brain speaks to itself without indiscreet witness ; it understands and perceives its own commands, without their being revealed to the external world, except by imperceptible muscular oscillations, of an intensity which varies greatly, according to the individual. This internal cycle probably duplicates the external cycle, not merely in internal and low, but also in loud speech, and takes part in what are called cinæsthetic impressions. It is thus at least that this sense of motor innervation, which some have maintained to be on an equality with the muscular sense, may be understood, and this without infringing the most fundamental laws of the nervous system, namely. that of the propagation of the impulses in a definite direction, and that of the distinction of the two opposite currents ensuring this propagation.

We can imagine all communication interrupted between the organs of the senses and their nuclei of origin, and at the same time between the motor nuclei and the muscles ; still, internal speech would not on this account be suppressed, any more than thought, which it interprets to us under a conscious form.

1. **Intelligence and consciousness.**—Consciousness and intelligence are closely connected, and we see that those beings who are the most self-conscious are generally at the same time the most intelligent ; but consciousness and intelligence are, nevertheless, distinct from each other. Consciousness involves an idea of *actuality :* it is this which enlightens the internal operations of the mind ; it ceases to be an actuality when these operations are withdrawn from this internal enlightenment. No explanation can be given of so elementary a phenomenon ; it embraces itself in its entirety, containing and contained.

Intelligence involves an idea of *capacity :* it may be estimated by the number, the complexity and the organization of the internal representations, images, and ideas that the mind in the course of its innumerable experiences is susceptible of acquiring. It is developed in the consciousness, but survives it as long as the organization of the representations subsists in its first perfection. The mathematician

who seeks the solution of a problem has only the principal relationship between the values present in his consciousness.

2. **Attention.**—Phenomena conveying the sense of spontaneity are, of all others, the most difficult to explain. In fact, they seem to be in conflict with the ordinary laws of causation, such as they appear to us in the physical world, and such as we wish to extend them to all phenomena whatsoever with the aim of unification. Attention, will, all the acts in which psychical *effort* takes part, are of this nature. It is true that in a large number of cases this idea of spontaneity is partly dissipated by analysis, as being a delusion. The sense of tension which we experience is really a psychical phenomenon, but it is a secondary one ; it is a sensation which arises, at least in part, from the involuntary tonic contraction of our muscles. If the attention seems of itself to be directed to an external object or an internal representation, it may also be aroused by an external or internal excitation in the same direction.

Attention increases the degree of consciousness ; it carries it in a given direction, which grasps it, or, as is often said, concentrates it ; that is to say, exalts it as regards a certain sense (sight, hearing, etc.), and diminishes it to the same extent as concerns others. The period of its perception is a very short one. For example, with regard to a sound first heard, this period has a given duration : for a second sound which the ear anticipates, it may be diminished by half and, the stimulus being the same, the sensation is equally intensified. At the same time, the residues of anterior sensations are recalled and swell the flood of new impulses circulating in the nervous system. While it lasts, attention suppresses the motor acts, and inhibits the muscular organs. This suspension of motor impulses favours the deliberation which takes place in the mind. The unknown once placed aside, the impulses which the attention has heaped up by momentarily suspending them, are launched on a career towards a distinctly determined end, and the motor acts prepared by the tension are executed.

At the same time that these changes take place in ourselves, in what we call the activity of the mind, others, more or less visible, are the consequence of it as regards the exercise of our functions both internal and external. We have just pointed out that the muscular tissue and the motor apparatus take an obvious part in the function of attention. Not only is its attitude a special one, but also its aptitudes are modified. Like physical labour, intellectual labour if prolonged brings about *fatigue*. Although not precisely similar in both cases, the analogies and the resemblances are great. This results from the fact of *intellectual and physical labour never being entirely independent of each other*. Sometimes one and sometimes the other predominates more or less, according to circumstances.

3. **Fatigue.**—The different conditions of the production of fatigue have been carefully studied by Mosso.

If, by repeated and equal excitations, we compel a muscle to yield the same contraction, and the amount of this contraction be registered each time, after a certain period, its loss of power, and finally its total exhaustion, will be rendered evident by the lessened elevation of the tracings on the paper. The line which joins the superior extremities of these tracings is the *curve of fatigue* (Kronecker). It is the more marked in proportion as the fatigue is the more quickly produced. It may then be considered as an evidence and an estimation of the fatigue itself. The experiment is carried out on a finger, the movements of flexion of which are made use of to raise a given weight. The myographic apparatus adapted to this test is an *ergograph* (a register of work done); this kind of myography adapted to the special study of fatigue and the diverse conditions of its production is *ergographia*.

Each rise, each double tracing inscribed by the elevation and the descent of the lifted weight, is a *test of force* capable of estimating the maximum labour. The whole, that is to say, the curve of fatigue, is a test of endurance, and is the most interesting.

We have an instrument with which we can estimate fatigue; we see the latter produced as the result of repeated efforts. Where is it situated? In the muscle itself or in the nervous system? And as this latter is complex, in which of its segments and superposed systems? The problem is a complicated one. Fatigue is both an objective and a subjective phenomenon.

Objectively, fatigue is ultimately a destruction (not sufficiently compensated by the converse current of reparation, which is never wanting). Direct analysis attests that it is especially in the muscle that this destruction goes forward, as the muscle is the great spendthrift of physical energy accumulated in the organism.

Subjectively, fatigue is a painful *sensation*, of which the approximate condition lies in the impression aroused by the destruction of the fatigued organs, in the sensory nerves with which they are provided. From this point of view it is nervous and cerebral. The nervous system takes part in the concatenation of the phenomena in order to arrest the cause of the movement, by suppressing the impulse which it transmits to the muscular system, and so stopping the destruction which would be the consequence of it.

Fatigue may be differently felt by different individuals, according to their peculiar sensibility. One will complain of a marked fatigue when the destruction has hardly commenced, another does not feel any fatigue when the destruction is far advanced; and when these differences are very marked, they are both prejudicial, as they denote and occasion a want of equilibrium in the functions. Sensation does not play its part, which is not only to excite, but also to weigh, regulate, and economize movement. Thus it is in the healthiest subjects that the sensation of fatigue, or, in one word, fatigue, best exerts its moderating action by arresting muscular effort.

Secondary effects of intellectual activity.—Thus physical work induces a psychical condition which keeps it within bounds by the operation of one of the funda-

mental reactions of the nervous system. Intellectual labour, in its turn, is the cause of a physical waste, much less, it is true, but still appreciable. The absence of movement of the muscles during the exercise of attention does not always imply their inactivity, but often conceals a certain tension. In this respect there are great differences, according to the individual and also to the degree of effort which accompanies the exercise of the attention. In some a relaxation of the fingers may be observed (MacDougal). In every case intellectual activity modifies the aptitude of the nervous system to give rise to muscular contractions. This is made manifest by the ergographic test when applied at the end of difficult and prolonged psychical labour. The curve of fatigue appears with much greater rapidity. Just as excess of physical labour temporarily diminishes intellectual activity or aptitude, so does excess of intellectual labour diminish physical activity or aptitude. We say excess, for if fatigue be avoided the contrary results : a small amount of work increases the muscular force, and this augmentation is evidenced by the test of endurance and also by that of force.

The reaction of psychical effort carried so far as to induce fatigue does not confine its effect to the external motor apparatus : the system of organic life also feels this reaction. During the exercise of attention, the pupil dilates (Mentz), the convergence of the two eyes diminishes, and the crystalline lens becomes flattened (Heinrich) ; the body temperature may also be increased (Gley).

The *circulation* and the *respiration* undergo modifications. A short and energetic intellectual effort produces cardiac and respiratory acceleration, and a vaso-motor constriction of the peripheral vessels, followed by a slight slackening of these movements.

An intellectual task lasting several hours, the body being in repose, causes weakening of the heart's action, and a contraction of the peripheral capillary circulation. This contrast is also observed in muscular exercise, only the figures are changed in value.

Effects on the cerebral circulation.—But the most interesting changes in the circulatory systems are those affecting the brain. If the cerebral and the radial pulse are simultaneously compared (in a case of loss of a portion of the skull), it will be found that, during intellectual activity, only the amplitude of the former is augmented (Mosso). The same thing has been observed by comparison of the radial and the carotid arteries (Gley). The brain increases in volume from the fact of its augmented circulation. Hyperæmia of the brain is not only a consequence, but also an effect of cerebral activity (Morselli). Like other organs, the circulation in the brain is adapted to the functions of the latter, and is regulated by them. The brain, though a nervous organ, which is both a receiver and dispenser of impulses, of which it maintains an inexhaustible reserve, is none the less subject to the same law as other organs. It is through the spinal cord and the great sympathetic that it sends to itself (to its vessels) the vaso-motor impulses which govern its circulation (recurrent motricity) ; it is by the medulla oblongata and the trigeminal nerve that it conveys in a contrary direction the sensory impulses which take part in this controlling cycle (recurrent sensibility).

B. LANGUAGE AND CEREBRAL LOCALIZATIONS

The mental mechanism of which, by the enlightenment of our consciousness we have an internal perception, is presided over by a physical mechanism which, in the brain of a being distinct from ourselves, would appear to us as being matter in movement, if we were possessed of physiological methods sufficiently perfect to unveil to us the delicate

and innumerable modifications which take place in the course of all these actions. But we are far indeed from the attainment of such a result. Nevertheless, a start has been made as regards the performance of this analysis, in so far as portions of the brain which preside over certain functions or operations of the mind are differentiated.

We already know that each specific sensation (each particular form of sensation) is located in a special system which, were it entirely abolished, would cause all trace of the corresponding sensations to disappear, and at the same time would prevent all possibility of their renewal. We also know that mutilation effected at the periphery of such a system, by separating it from its normal stimulus, renders impossible that formation of physical images which is essential for the renewal of the sensation, but allows of the subsistence of the psychical images stored up in the memory. We also know that, conversely, the removal of determinate regions of the cortex, which are the culminating points of each of these systems—while permitting the renewal of the stimulus at the periphery, and also the persistence of certain reflex automatic or instinctive manifestations, of unconscious or subconscious nature, which are united to the organization of the sub-cortical portion of the system—destroys the provision of corresponding psychical images.

Pathological dissociation of the elements of language.—But the visual, like the auditory, images are more or less complicated representations. Below the images properly so called, exist sensations, which are their elements. The images resulting from their grouping are, some, concrete (images of objects), others, symbolical or abstract (verbal images, or those of language whether spoken or written). Pathology demonstrates that some of these images may disappear, while others are preserved more or less unaltered. The disappearance thus effected may concern the sensations or images of a given sense, while allowing of the subsistence of those of other senses ; a choice may also be made between the more or less complicated orders of the different images or representations of this sense. It may, for example, suppress the verbal images of hearing or of vision, while allowing the images of objects to persist, and naturally also the sensations, in a more or less partial manner. It may suppress all the psychical images and only permit the sensations to remain ; and, finally, it may destroy the psychical manifestations of a sense so utterly that nothing of it remains.

Aphasia.—When the disturbance of which the brain is the seat is limited to the suppression of verbal images, aphasia ensues. The person suffering from aphasia is not also the victim of aphonia, for he preserves intact the motor powers of language, though he is incapable of using them. Neither is he to be considered as mentally affected, for he possesses ideas which he is incapable of expressing. A disturbance of this nature, which respects both the inferior sensori-motor activities and also to a certain extent the formation of ideas, is necessarily a local disturbance. It is indeed seated in the brain and, further, it only affects in this organ one of the systems participating in the function of language ; for, were it to involve all these systems simultaneously, it would not be the expression of the idea alone, which would disappear, but also the idea itself. As ideation has many sources (audition, vision . . .) and equally numerous means of expression (speech, writing . . .), it persists, but in, it is true, a more or less shattered condition. A person suffering from aphasia is an individual who has not lost the whole function of language, but one of the factors taking part in this complex function.

The lesion giving rise to aphasia presents distinct anatomical and functional forms. Sometimes it destroys, in the cortex itself, the partial systems which

give rise to verbal images (*cortical aphasias*). Sometimes it interrupts the communications of these systems with each other, or with the inferior systems for the reception of sensation, or for the performance of movements (*aphasias of conduction*). But, even in the brain, we distinguish between systems for the reception and organization of sensations and those for the performance of motor verbal function ; whence, according to the seat of the lesion in one or other system, we find two functionally different forms of aphasia, one *sensorial* and the other *motor*.

1. Aphasias known as cortical

Some verbal images are sensorial and others motor. The first are more or less complex representations, which are awakened in us in a passive manner at the instigation of the signs (audible or visible) of language. They fully merit the name of images, because they are spread out in the open light of consciousness, and lend themselves to internal analysis. The second resemble them inasmuch as they also are associations, ready prepared and easily to be evoked ; but they differ from them in that their cerebral mechanism eludes a subjective analysis, and that the representations caused by them are secondary, that is to say, posterior to the physical or muscular act which they determine or solicit. They are only images in a metaphorical sense.

Further, the sensorial images are not entirely free from motor effect, if only those movements of adaptation are taken into account which are necessary to the functional activity of every organ of the senses at the moment when the stimulation falls on it ; any more than the motor images are quite free from sensory effect, on account of the impulse which, from the muscles, ascends to the brain to register the accomplished movement.

Language, which is a complex function, associates sensori-motor cycles into a cycle of aggregation. In this association some of these partial cycles assume essentially a sensorial function (auditory or visual system), and others essentially a motor function (tactile systems). As these systems are localized in distinct regions of the brain, it follows that, according to the system involved, the aphasia will be either sensorial or motor.

A. Motor aphasia.—In the gradual development of the question, the aphasia styled motor was the first to be observed ; and it is connected, as is well known, with the problem of the functional localizations of the brain. Broca has proved that *loss of articulate speech is the result of the destruction of the third frontal convolution of the left hemisphere.* The individual thus attacked preserves his intelligence. If the lesion does not transgress the limits just indicated, he may be immune from all motor paralysis ; the emission of sounds is possible ; the apparatus of phonation, properly so called, is intact ; but although

the patient is conscious that he might turn it to account for the communication of his ideas, it is impossible for him to make use of it. He retains the faculty of internal language, but external language is impossible.

This incapacity is explained by saying that he has lost the motor memory of the articulation of words. His store of motor images of articulation is destroyed from the fact of the destruction of the third left frontal convolution.

Agraphia.—It may sometimes happen that, while speech is preserved, writing is impossible: this is called *agraphia*. An attempt has been made to localize the lesion of this disturbance of language in the foot of the *second frontal* convolution (Exner); but this localization has been disputed.

B. Sensorial aphasia.—Wernicke subsequently distinguished a new form of aphasia, called by him "sensorial," which differs from the preceding by its symptoms and the seat of the lesion. The person affected by this form of aphasia can articulate sounds or write, and may even be verbose; but the disorder of language is shown by the fact that his words have no meaning, or do not answer to the question put to him. Sometimes he has lost his verbal auditory images (word deafness), and it is in this case that sensorial aphasia is most markedly evident; sometimes he has lost his verbal visual images (word blindness), and the disturbance of the function of language is rendered manifest by his inability to read. The written signs have, for him, lost their symbolical signification; he can write, but cannot read what he has written; he can speak and answer an oral question, but not a written one.

Word deafness.—Word deafness is observed in the case of injury to the *first temporal convolution* on the left side. The area of the cortex which originates verbal auditory images thus includes almost the whole of the terriotry of audition; a limited lesion of the left side allows of the persistence of the sonorous sensations or of pitch, while destroying its symbolical significance.

Word blindness.—Word blindness is observed as the result of destruction *of the left inferior parietal lobule* with or without participation of the *angular gyrus*. It therefore usually accompanies agraphia. Pure word blindness, without being complicated with agraphia, has been observed in the case of interruption of the *inferior longitudinal tract* of Burdach (inferior portion of this tract).

It seems, therefore, as if the fibres of the longitudinal tract were employed to put the cortical area of vision into communication with the area of language (Dejerine). The homonymous hemianopsia which

accompanies this lesion is due to the concomitant atrophy of the optic radiations.

Verbal auditory amnesia.—Word deafness is a permanent lesion, at least in the conditions under which it is usually observed ; but it sometimes displays itself in a transitory and attenuated form, either under toxic influences, such as that of tobacco (G. Ballet), or by the progress of old age. For if our store of internal experiences always goes on increasing, we have more and more trouble in making use of it, evocation of words being performed with difficulty and sometimes uselessly. And it is under these circumstances that their disappearance follows a fairly regular order, proper names being the first to go, then common nouns, while adjectives and verbs are remembered.

Visual verbal amnesia.—This is less well known than the preceding, and always difficult to differentiate from other disturbances of the same nature, and, very exceptionally, it occurs in a transitory form.

Sensorial types.—Hearing is the sense usually employed for the registration of verbal images, on account of the infinitely greater use we make of speech than of writing. Sight, on the contrary, is the sense which registers the images of objects, because vision has in this respect a permanence of action and a precision which hearing does not possess. But there are individuals in whom internal speech, or the operations of the mind, more resemble reading than internal audition ; these persons are called *visuals*, in opposition to *auditives*, in whom auditory images have an almost exclusive preponderance and use. Further, *motors* are distinguished, in whom internal speech would be the representation of a movement of articulation, and the *indifferent*, in whom these various images would be employed according to circumstances. These distinctions, established by Charcot, and to which exception has sometimes been taken, are considered as fundamental by a fairly large number of neurologists.

Amusia.—Music also is a language, but one that is expressive of emotions, and not representative of ideas. In any case it has its symbols, which form in the musician a store of musical images. It is possible for these images to be lost in the same way as verbal images.

Amimia.—Mimicry is a language more primitive and more general than language properly so called ; it is possible for the images of mimicry to be lost. Brissaud describes an *aphasia of intonation*.

2. Aphasias from default of conduction

Aphasia, in its different forms, is brought about by lesions of the cortex, the seat of which we have just pointed out. To each of these regions is attributed a power of preservation of those images, either

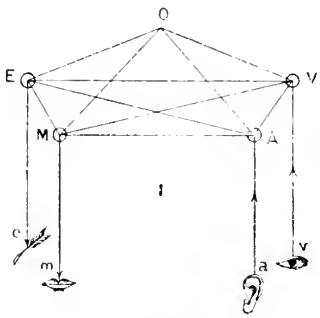
sensorial or motor, which take part in the function of language. It is even generally maintained that these images are included therein. This manner of propounding the localization of language and its principal mechanisms goes beyond the ascertained facts. These latter incontestably prove that each of these regions is an essential portion of the nervous mechanism of language. But this mechanism is capable of being changed and arrested as regards its function by lesions other than those of the cortex. For aphasia to be produced, it is necessary and sufficient that the principal associations presiding over the function of language be interrupted. In some points this rupture is brought about by the destruction of certain regions of the cortex; but it may also be induced by interruption of the white tracts, whose definite function it is to mutually associate these regions, or by that of the fibres of projection terminating in them or immediately leaving them. These are called the *aphasias* of *conductivity*.

Essential difference.—The symptomatological difference lies in the important fact, that *internal language*, corresponding to the loss of the images whence aphasia results, *is then preserved*. There is no obliteration of an order or a form of images, but rupture of the connexions which must normally exist between these images for speech or for writing to be properly carried out. To put it otherwise, the internal organization of the partial systems which ensure the formation of motor or sensorial images (organization carried out by the above-mentioned regions of the grey matter) is not compromised, but there is a separation of these different systems, together with the impossibility of uniting in common functions for the future (associations effected by certain fibres extending in a large number from one to the other of these regions through the white matter). Injuries affecting the region of the insula, situated immediately between the regions called sensorial and those called motor, produce aphasia of this nature by section of the white tracts of association passing through it (Dejerine).

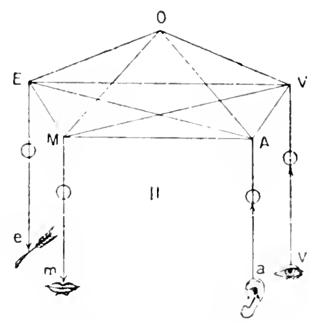
Schematic constructions.—Charcot, Lichteim, Grasset, and several other authors have constructed schemes intended to facilitate the comprehension of the mechanism of language, as well as its disturbance in different aphasias. That of Grasset, inasmuch as it aims less at the clinical reality of the different disturbances observed, is the one most appropriate for the concrete representation of the different questions discussed with regard to the analysis of language in its normal or disturbed condition. By connecting together the four cortical centres (two for sensation, two for motion) which preside over this function, a sort of horizontal polygon is produced, of which these areas of the cortex form the angles. From these same angles start ascending vertical lines, to represent the sensorial nerves, and descending lines for the motor nerves. By the associations here produced between sensation and movement, this polygon ensures both the physiological and psychological automatism of the functions of language. But these

functions are not entirely automatic : they are sometimes intellectual. Hence each of these centres is once again joined by lines to a superior centre, to that of intelligence.

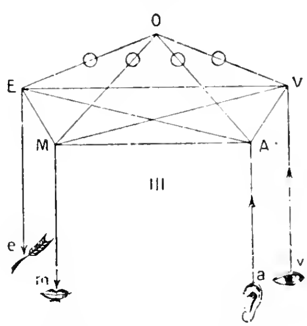
Without speaking of the destruction of the centres themselves, the interruption of the conductors may be either intra-polygonal (separation of the centres in automatic function), sub-polygonal (separation of the centres from their peripheral connexions), or supra-polygonal (separation of the polygonal centres from the superior centre of ideation), and the symptoms vary accordingly. Anatomically, all these centres are situated in the cortex, while all the white fibres connecting them (both mutually with the inferior regions, and with the centre of ideation) are located below the cortex. By giving to the expressions a symbolical mean-



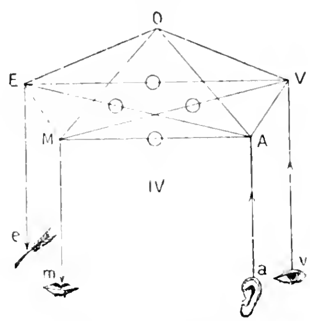
Cortical Aphasias.



Sub-cortical Aphasias.



Supra-cortical Aphasias.



Trans-cortical Aphasias.

FIG. 261.—Diagrams representing the different classes of aphasias and the different forms which they may individually assume.

I, II, III, IV, four classes of aphasias, according to the seat of the lesion, whether in the grey matter (special centres), in the white matter (in the course of the fibres of projection of these centres), in the white matter (in their tracts of mutual association), in the white matter (in their tract of communication with the superior centre of ideation).

A, auditory centre ; V, visual centre ; M, motor centre of articulation ; E, motor centre for writing ; O, intellectual centre (after Grasset).

ing which elucidates their function, Grasset calls the intra-polygonal fibres *trans-cortical*, the sub-polygonal *sub-cortical*, and the supra-polygonal *supra-cortical*, all of them converging towards the centre O, or superior centre of ideation.

Principal differences—1. Cortical aphasias and those of conduction.—Between cortical aphasias and aphasias the result of lack of conduction, the difference is that, for example, in the first, one of the systems presiding over the formation and conservation of verbal images (auditory, visual, motor) is destroyed as regards

its essential portion (corresponding cortical centre); while in the second these systems persist. In the first case the images disappear; in the second they are preserved, and only lack the power of forming certain connexions between themselves and with the external world. Thus *cortical aphasias are more serious than the aphasias of conduction*, since, in them, the group of images is no longer connected in a definite manner, but, further, its function has disappeared.

2. **Sub-cortical aphasias.**—*In sub-cortical aphasias internal language seems to be almost intact.* All images persist; but if the sub-cortical lesion is in one of the two sensory fields, they are not renewed in the corresponding area; if it is in the motor field, they are no longer expressed, or are expressed by a new conventional gesture language.

Anarthria.—If the lesion is situated somewhat lower in the corona radiata, in the vicinity of the internal capsule, it is no longer aphasia, but *anarthria* or *dysarthria* which is observed (defect of articulation).

3. **Trans-cortical aphasia.**—In trans-cortical aphasias, all the verbal images persist, but their mutual sensory or motor connexion can no longer be definitely effected. Hence it follows that certain varieties of *automatic language are affected* (reading aloud, repetition, ordinary copying, or copying from dictation). Conscious voluntary speech is, on the contrary, possible by means of the both indirect and complicated connexions formed between the sensorial and motor images.

4. **Supra-cortical aphasias.**—In the aphasias known as supra-cortical verbal images still persist, they are renewed and expressed by means of the connexions maintained with the periphery, and are mutually evoked (from the sensorial to the motor) in automatic language; but connexions of a slightly different nature are then partially interrupted. The passage from the image to the idea, or conversely from the idea to the image, in any one, or in several, forms of sensation has become difficult or impossible. *The idea exists and also the image, but the one cannot call up the other, or conversely.*

Seat of ideation.—The most ill-defined centre, anatomically and functionally, is that known as the centre of *ideation*, which is represented in most schemes, including that of Charcot, as being isolated from the others. It seems to me that the expression " centre " should be here especially considered as being purely symbolical. Less than any other, can the function of " intelligence " be concentrated and localized in a definite region of the brain (for example, in the frontal lobe).

Doubtless, when substituted for the psychological automatism, it is brought into being in the cerebral cortex by an *extension* of already associated systems, which in the aggregate includes new portions and new systems, solidarized into a complex association; but we are not authorized in maintaining that these superadded systems (which may be called supra-cortical centres) would subserve the intellectual function were they completely isolated. Further, the conception of a centre of ideation is only brought forward for the purpose of simplifying and classifying facts.

Automatism and intelligence.—It is certain that, in apparently similar disturbances of language, intelligence may be affected in a somewhat diverse manner.

Much diminished in some cases, it may be left almost intact in others. We have said above that, in aphasias of conductivity, it is much better preserved than in aphasias the result of cortical destruction, the mechanism being much less involved in the first than in the second. Sometimes a kind of dissociation may be observed between intelligence and speech, the latter being automatic and effected without comprehension of the words spoken, intelligence nevertheless being manifested in an indubitable manner.

There is then, in this case, a separation between external language (become automatic) and internal language (which represents ideation). It is scarcely possible to maintain that this functional dissociation corresponds to a *total* isolation of the seat of ideation, which would then be left without any connexion with the exterior. In such a case intelligence would be necessarily and very seriously affected ; it is much less so when one of the areas for the formation of verbal images, auditory for example, is destroyed. In the aphasias by default of conduction, and especially in those called supra-cortical (supra-polygonal according to the diagram), it would seem that the connexion between the different partial areas of language is less gravely involved than in cortical aphasias, although certain ways of passing from the word to the idea and from the idea to the word become impossible. By the fact of this connexion being less disturbed, the preservation of internal language and of more complete ideation in these forms of aphasia may be explained. Whence it follows that it is this connexion, together with probably an extension of the associations in the cerebral substance, which forms the essential condition of ideation.

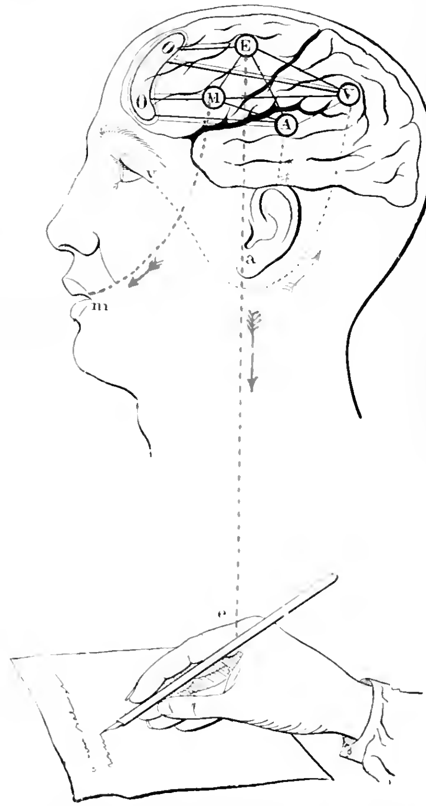


FIG. 262.—Centres or systems of language and their principal associations.

A, auditory centre ; V, visual centre ; M, motor centre of speech ; E, motor centre of writing ; OO, intellectual centre.

Sensory nerves in blue ; *aN*, auditory nerve ; *vV*, optic nerve. Motor nerves in red ; M*m*, nerves of phonation ; E*e*, nerve of writing (after Grasset).

3. The area of language, its constitution

Anatomical and clinical analysis has, as we have seen, defined three partial areas in the cortex (three centres) : one for auditory, one for visual, and one for motor images of phonation, and yet another, a fourth, if we include the centre for writing ; to all these areas distinct functions as regards language have been attributed, and they were formerly considered as being independent.

The subsequent investigations of Freud and Miraillé have tended, while upholding their functional differences, to point out the connexions which these areas maintain between themselves, and also with the neighbouring areas of the cortex. These authors maintain the existence of an area of language, of which the centre for motor images (base of the third frontal) occupies the anterior portion, the centre for verbal auditory images (first temporal) the postero-inferior portion, the centre of verbal visual images (parietal lobule and angular gyrus) the postero-superior portion. These centres are mutually connected by fibres of association, which thus make of them a complex whole, so that the individual lesion of each involves a general disturbance of all, but with marked predominance in the function corresponding to the centre

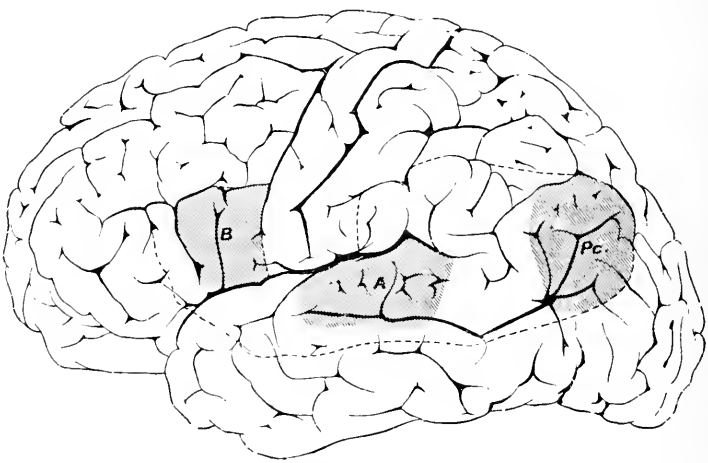


Fig. 263.—Area of language and its three centres of images (after Dejerine).

A, centre of the auditory images of words (centre of Wernicke); B, centre of the motor images of articulation (centre of Broca); Pc, centre of the visual images of words.

A dotted line indicates the limits of the area of language as a whole.

affected by the lesion. They also observe that each of these centres is in direct relation with an area of the cortex, which acts as a storehouse for general impressions belonging to the same category. Broca's centre is in contact with the general motor area, at its inferior portion, in the vicinity of the cortical origins of the hypoglossal nerve, the facial nerve, and the nerves supplying the muscles of mastication (nerves of the face, the lips, the soft palate, the tongue, the larynx and the pharynx). The centre for visual images is connected with the centre of general vision by its deep surface, and comes in contact with the optic radiations. The centre for auditory images is almost identical with that of general audition. In short: according to this theory *each centre is a portion of the neighbouring area, differentiated and appro-*

priated to the specialized function of language. As, on the other hand, the connexion between these different sensorial and motor centres is a close one, *isolated lesion of each of them is rendered evident by predominating disturbances of its own proper function, and these also react, but in a feebler manner, on the functions of the other centres* (Dejerine).

Fibres of association.—Of the fibres of association of the area of language some are *short*, passing from one convolution to another, and others are *long*, uniting this to other cortical areas. Amongst them may be defined a superior longitudinal or arched tract; an occipito-frontal tract extending between the frontal lobe, the insula, and the temporo-occipital lobe (forms the *tapetum*); an inferior longitudinal tract which unites the visual occipital area to the temporal lobe. The area of one side is united to that of the other by the inferior portion of the body of the corpus callosum.

Fibres of projection.—From the area of language fibres of projection extend to the optic thalamus. A fronto-thalamic tract occupies the anterior segment of the internal capsule. The fibres of the third frontal convolution, and of the adjacent region, form the knee of the internal capsule (anterior portion of its posterior segment); in the crusta (*pied*) of the crus cerebri they occupy the antero-internal and the internal border.

C. PROCESSES AND ORGANS OF ASSOCIATION

Experimental and clinical analysis when applied to the brain proves the existence of an obvious functional differentiation between its different portions. The removal of certain determinate areas of the cortex abolishes, or at least degrades, specific systems, the activity of which altogether ceases or becomes unrecognizable. An impulse, when artificially caused to penetrate these areas, reawakens this activity, and renders it manifest by motor effects. These territories, however, such as they have been delimited by experiment, are not continuous, but leave between them a space of irregular outline, to which the name of *latent* or inexcitable area has sometimes been given. As is obvious, it is more especially by its negative characters that this distinct territory is defined. Its destruction does not involve sensory or sensorial anaesthesia, and does not bring about a motor paralysis; and its stimulation is not revealed by any externally visible signs.

Anatomical hypothesis.—The alternative lies between the following hypotheses: either this area described as inexcitable is fundamentally equivalent to those which crown the sensorial systems known as specific, only its sensomotricity is of an order which we are incapable of recognizing; or else it clearly differs from those appertaining to these specific systems and presides over functions into which the diverse sensibilities and motricities no longer enter as distinct and recognizable elements, but are, on the contrary, mingled together in different ways.

The second of these two hypotheses is the one which has had the widest acceptation. A support for it, and in a sense a demonstration of it, has been found in the anatomical fact, first affirmed by Flechsig, that this inexcitable area (itself decomposable into a certain number of special areas), being deprived of fibres of projection, is, on the other hand, rich in fibres of association, both long and short, which bring it into connexion with the specific areas of the different senses. In a word, its function would thus be, not to associate the cortex with the functional activity of the grey axis, in motor or sensory transmissions, but to connect the sensori-motor cortical areas, and in this way to derive from them new mani-

festations of a superior psychism. So these territories, which make no response whatever to direct stimulation, would be centres of ideation.

Objections.—The anatomical fact brought forward by Flechsig has been strongly criticised by several authors (C. and O. Vogt, Mahaim, Sachs, Dejerine, Monakow), and has been also partly abandoned by himself.

Experiments.—Demoor has striven to clear up this question by the following experiments. He destroys the cerebral cortex in different dogs in the following manner : (*a*) in the tactile area (sigmoid gyrus) ; (*b*) in the visual area (occipital lobe) ; (*c*) in the frontal lobe ; (*d*) in the parietal lobe (these two latter regions being described as centres for the association or the formation of ideas, by comparison with the two former,which represent centres of projection). The results observed (symptoms of deficiency after cure) have been as follows :—

a. *Ablation of the tactile area.*—Sensibility and motricity persist with the essential modifications observed in such cases. The character is changed, and the animal becomes aggressive. *Intelligence is absolutely ruined.* Neither by touch, hearing, sight nor smell can the animal be induced to perform any intelligent act ; it may be considered as being in a condition of dementia.

b. *Ablation of the visual area.*—First of all, psychical blindness appears (cortical blindness), then vision becomes, after a certain time, at least partially re-established. The dog then presents a normal appearance and is capable of the education or intellectual acquisitions of an ordinary dog.

c. *Ablation of the frontal centres.*—Except for a slightly increased excitability, which disappears after some days, no change from the normal condition can be noticed.

d. *Ablation of the parietal centres.*—When in a locality which is known to it, the animal appears to be in a normal condition ; but it presents serious anomalies when in an unfamiliar place ; it experiences great difficulty in ascending a staircase and is incapable of descending ; it is also incapable of learning how to " give a paw."

From the last experiment the author infers that the parietal centre really possesses a function of association of the nature of that which has been attributed to it ; it would, then, in the dog be the co-ordinating centre of the elementary intellectual activities. The frontal centre has only very slight influence, and that not a recognizable one, this being the result of its very rudimentary development in the carnivora ; this centre being phylogenetically (and ontogenetically) of very tardy development, and only acquiring importance in the primates and more especially in man.

It must be observed with regard to this subject that the frontal lobe of the ungulata is highly developed in comparison with that of the carnivora, and this obviously without the intelligence of these animals profiting from this development (Monakow).

With regard to the parietal centre, we cannot help remarking that, if its destruction has brought about a disturbance in the association of ideas and intelligence, this disturbance is incomparably less marked than that resulting from the destruction of the tactile area ; and yet, in the latter case, the animal retained not only its parietal and frontal centres of association, but four out of five of its senses remained to furnish it with sensations, two of them being superior senses, namely, sight and hearing.

Moderating functions of the frontal lobe.—Bianchi, as the result of the removal of the pre-frontal region in the monkey, maintains that a certain condition of mental inferiority ensues. The experiments of this author, those of Goltz on the dog, and an observation of Harlow on man, all tend to show that destructions affecting the anterior portion of the brain produce a modification of character, causing it to become impulsive, irritable, and incapable of exerting self-control.

Inhibition.—R. Oddi, and, later, G. Fano, operating on the dog, have proved that stimulation of the frontal area, which is considered inexcitable, has an inhibitory influence on the movements elicited by reflex stimulation. Fano, after ablation of the cortex in this region, finds that the latent period of the reflexes is diminished. This is more especially a crossed action, and one more obvious in the anterior than the posterior limb. As regards the first, the time occupied by the reflex, which is from 32·6 to 36·9 thousandths of a second, becomes, some days after the operation, 23·8 to 26·1 thousandths of a second.

In spite of their interest, these facts throw but a feeble light on the function of the brain taken as a whole. Apart from a functional differentiation which affects certain of its regions and of the links which unite certain specific territories in the area of language, it must be admitted that we know very little concerning this function.

D. SLEEP.

Sleep is a suspension, a more or less complete interruption, of conscious and voluntary activity. The external senses are partially closed, or are voluntarily sheltered from stimuli arising from the external world. The body assumes, preferably, a horizontal position and remains almost motionless. The respiration, the circulation (slightly slowed) and the general nutritive activity pursue their regular course. The eyelids are closed, and the pupils being contracted, the eyes are turned upwards and inwards.

Dreams.—Mental activity is not entirely abolished ; the occurrence of dreams, many of which leave a more or less distinct impression in our memory (often very slight, and no doubt frequently entirely effaced) is a proof of this being so. Mental activity in dreaming is based on previous excitations of the nervous system, which have remained stored up in it in an unconscious state, and to which, during sleep, are added the slight excitations accidentally arising from the senses in spite of their state of repose (external noises, pressure of the body on the skin and the limbs, internal excitations having their source in the viscera, etc.). When awake, these sensory or sensorial excitations are superposed to previous residual excitations of the same nature, which they recall in a logical order, according to certain laws. In dreaming, on account of the lowering of the cerebral activity which is essential to sleep, these associations are formed, as it were, haphazard, whence arises their instability, as well as the well known extravagance and incoherence of dreams (Bergson).

Supposed mechanism.—With regard to the manner in which the disaggregation of cerebral systems is brought about in sleep and their recomposition on waking, several hypotheses have been formed, some of a chemical order (ponogenic substances of Preyer), others of an anatomical nature (histological theory of M. Duval). Nevertheless, the mechanism of sleep is still obscure and but little is known concerning it. During sleep the brain is relatively anæmic, so far as can be judged from observations made in men and animals who have been trephined.

Necessity of sleep.—The cause of sleep is also quite unknown to us. The nervous system is obedient to a law of periodicity which is imposed on the functions of all the organs and of their component elements, a law of which we can only declare the general application, but whose fundamental nature is unknown to us. Activity calls for repose, and reciprocally. The period of this activity followed by repose is modelled on the nycthemeron ; the time of wakefulness corresponding to day, and that of sleep to night.

Artificial sleep.—Sleep may be obtained artificially by the aid of certain substances, the narcotics (morphine), the anæsthetics (chloroform, ether, etc.).

Hypnotism.—In individuals manifesting hysterical symptoms (anæsthesia, hyperæsthesia, etc.), the condition called hypnotism is easily induced by stimulations directed to certain senses, such as passes made with a magnet, fixation of the eyes on a brilliant object, pressure on certain points of the cutaneous surface, etc. Re-awakening is obtained by similar means (blowing on the forehead, pressures . . .).

The individual passes generally through three phases, which may, however, sometimes occur separately, namely: the *cataleptic*, the *lethargic*, and the *somnambulistic* condition. In this latter condition the individual deprived, in a sense, of his ordinary personality, presents a really remarkable automatism, and obediently follows all suggestions proposed to him, even when these imply the performance of acts taking place at a more or less remote date, and which must be carried out after his awakening. *Hypnotism*, *magnetism*, or *Braidism* consist in conditions involving a mental depression or resolution, which causes the elimination of the superior functions of the nervous system, including distinct consciousness, and more especially will, and only permitting the persistence of an activity which is, in a sense, purely automatic.

Personality; its disaggregations.—Hypnosis, inasmuch as it is a condition which can be elicited at will in some hysterical subjects, has to some extent rendered possible the analysis of psychical phenomena. It proves that *the ego is an association of differentiated and co-ordinated elements* (Ribot, Binet, Janet). This association does not occupy the whole of the organism, nor the whole of the nervous system, but only a portion of it. It is not stationary, but eminently mobile and variable. It seizes without cessation on new elements, and eliminates others from its constitution.

Secondary personalities.—The elements which it leaves outside itself form secondary aggregations whose own individuality is unrecognizable, lost as they are in the general function in which they co-operate, although remaining external to consciousness properly so called. In hypnosis these aggregations are capable of attaining a degree of organization which brings them into a condition of secondary personalities co-existing with the *ego* properly so called, and quite distinct from it.

The *sub-ego* thus constituted hears questions which the *ego* does not perceive, and returns answers to them of which the latter is unconscious. The sensori-motor cycle of this special language may be retained in the tactile system (cutaneous stimuli or communicated movements initiating in answer intentional co-ordinated movements of the hand); or it may be more extended (words whispered in the ear giving rise to written answers in persons whose attention is, on the other hand, closely concentrated on a distinct object or subject).

Spiritualism.—The dissociation of the personality may in certain cases be less deeply seated. The question proposed may be known by the *ego* and be a conscious one, and the answer of the sub-ego be unconscious and involuntary; that is to say, it may nevertheless reveal an intelligence distinct from the preceding. This is the case with the mediums in those *séances* which are called *spiritualistic*. The belief in extra-somatic "spirits," which can be called up and communicate their thoughts through the organs of the "medium," is founded on facts of this nature. There is usually in these cases a separate intelligence (generally of an inferior order), which acts unknown to the veritable *ego*; but this intelligence occupies the same body, the same nervous system, and is nothing but an alienated portion of the intelligence of the "medium" which has assumed an independent condition, but still drawing upon it for a share of the common store of memories. The separation is sometimes pushed so far that these two intelligences may converse the one with the other, without foretelling the answer, as would two organically distinct individuals.

BIBLIOGRAPHY.

General sensibility.—Nerves and terminal apparatus.—Canini, Endig . . . Froschlarvenschwanzes, *Arch. f. Anat. u. Phys.*, 1883, p. 149.—Richelot, Distrib. des nerfs collat. des doigts. . . . *Arch. Phys.*, 1875, p. 177.—Ruffini, . . . Papilles . . . peau de l'homme, *Arch. it. biol.*, 1893, t. XVIII, p. 435.—Vanlair, Innerv. directe de la peau, *C. R. Ac. sc.*, 1886, t. CIII, p. 352.—Wolff, Tastkörper . . . *Arch. f. Anat. u. Phys.*, 1883, p. 127.

Spinal ganglia, posterior roots.—Cavazzani, Gangl. spinaux, *Arch. it. biol.*, 1897, t. XXVIII. p. 50.—Paladino, Résect. rac. post., *Arch. it. biol.*, 1895, t. XXIII, p. 146.

Cutaneous sensibility.—Bloch, Sensat. de traction et pression cutanée, *Arch. Phys.*, 1891, p. 322.—Boeri et di Silvestro, Dissociat. des différentes sensibilités sous l'action de différents agents, *Arch. it. biol.*, 1899, t. XXXI, p. 460.—Charpentier, Analyse exp. sensation de poids, *Arch. Phys.*, 1891, p. 122.—Dessoir.—Ub. d. Hautsinn, *Arch. f. Anat. u. Phys.*, 1892, p. 175.—Sig. Exner, Intermitt. Hetzhautreiz., *Arch. v. Pflüger*, 1870, p. 214.—Henri, Localis. sensat. tactiles, *Arch. Phys.*, 1893, p. 619.—Kiesow, Sens pression déform. de la peau, *Arch. Phys.*, 1896, t. XXVI, p. 417.—Wilh. Koch, Zur Lehre von der Hyperästhesie, *Arch. f. Anat. u. Phys.*, 1877, p. 475.—Laulanié, Durée de la sensation tactile, *C. R. Ac. sc.*, 1876, t. LXXXII, p. 1314.—Oehl, Critérium chronométrique de la sensation, *Arch. it. biol.*, 1897, p. 240.—Ottolenghi, La sensibilité et l'âge, *Arch. it. biol.*, 1895, t. XXIV, p. 139.—Pastore, Oscill. des sensat. tactiles, *Arch. it. biol.*, 1900, t. XXXIV, p. 262.—Roger, Excitat. cutanées, *Arch. Phys.*, 1893, p. 17. —Shore, Taste sensat., *Journ. of Phys.*, 1892, p. 191.—Schmey, Modific. d. Tastempfindung, *Arch. f. Anat. u. Phys.*, 1884, p. 309.

Muscular sense.—Cattaneo, Org. musculo-tendineux, *Arch. it. biol.*, 1888, t. X, p. 337. —Claparède, Thèse Genève, 1897.—Goldscheider, *Arch. f. Anat. u. Phys.*, 1889, suppl., p. 141.—Ruffini, *Arch. it. biol.*, 1893, t. XVIII, p. 106 ; *Journ. of Phys.*, 1898, p. 100.

Sensibility of the viscera.—Buys, Sensib. de l'ovaire, *Arch. it. biol.*, 1891, t. XVI, p. 87.—Pagano, Sensib. du cœur et des vaisseaux, *Arch. it. biol.*, 1900, t. XXXIII.

Thermic sensibility.—Cavazzani, Différenciat. de ses org. avec ceux de la pression, *Arch. it. biol.*, 1892, t. XVII, p. 413.—Goldscheider, Preuves diverses dissociation, *Arch. f. Anat. u. Phys.*, 1885, suppl. 1886, 1887, 1888.—Ch. Henry, Sensib. therm., *C. R. Ac. sc.*, 1890. t. CXI, p. 274 ; Relation sensib. thermique avec température, *C. R. Ac. sc.*, 1896, t. CXXII, p. 1437.

Visual innervation—Retina.—Fr. Boll, Abelsdorff . . . Helligkeit. und Farbensin, *Arch. f. Anat. u. Phys.*, 1900 ; Licht und Farbenempfindung, *Arch. f. Anat. u. Phys.*, 1881.—Charpentier, Vision différ. parties rétine, *Arch. Phys.*, 1877 ; Vitesses des réactions, *Ibid.* 1883 ; Sensations visuelles et auditives, *Ibid.*, 1890 ; Dissociat. impress. sensit. success. occupant le même siège, *Ibid.*, 1891 ; Réact. oscill. rétine, *Ibid.*, 1892 ; Oscill. rétiniennes, *Ibid.*, 1896 ; Sens lumin., *Rev. gén. sc.*, 1898.—J. Gad, Energieumsatz in Retina, *Arch. f. Anat. u. Phys.*, 1894.—Greeff, Morphol. und Physiol. Spinenzellen . . . *Arch. f. Anat. u. Phys.*, 1894 ; Längsverbind. in der menschl. Retina, *Ibid.*, 1898. —König, Farbenschen und Farbenblindheit, *Arch. f. Anat. u. Phys.*, 1885.—Kries, Gesichtsempfindung, *Arch. f. Anat. u. Phys.*, 1878.—Parinaud, La vision : le même, *Rev. gén. sc.*, 1898.—Rawitz, Cephalopoden retina, *Arch. f. Anat. u. Phys.*, 1891.

Chiasma.—Bechterew, *Neurol. Centralbl.*, 1898.—Cajal, *Rev. trimest. micr.*, 1898. —Gudden, *Graefe's Arch. f. Ophtalm.*, XX, 1874 ; XXI, 1875, et XXV, 1879.—Jacobsohn, *Neurol. Centralbl.*, 1896 et 1898.—Nigati, *Arch. de Phys.*, 1878.

Hemiopia ; hemianopsia.—Dejerine, Sollier et Auscher, Lésion écorce occipitale, *Arch. Phys.*, 1890, p. 177.—Wernicke, . . . Reichsettig. Hemiopie, *Arch. f. Anat. u. Phys.*, 1878.

Cortical visual sphere.—Monakow, Ursprungcentren . . . *Arch. f. Anat. u. Phys.*, 1885.—H. Munck, *Arch. f. Anat., u. Phys.*, 1879 et 1880.

Cortical sphere.—Bechterew, *Neurol. Centralbl.*, 1897.—Bouveret, *Rev. gln. opht.*, *opht.*, et *Lyon médical*, 1877.—Brissaud, *Ann. oculist.*, 1893.—Dejerine, *Biologie* (mémoire), 1892.—Henschen, Congrès internat. de Rome, 1894.—Lannegrace, *Arch. méd. expér.*, 1889.—Luciani et Tamburini, Sui centri psico-sensorieortiali, Reggio Emilia, 1879.—Monakow, *Arch. f. Psych.*, XIV à XXIV.—Munk, *Akad. d. Wiss. Berlin*, 1890. —Schäffer, *Brain*, 1888.—Scherrington, *Journ. of Phys.*, 1894.—J. Soury, Les fonctions du cerveau, 2e édit., 1892 (Ind. bibliogr.).—Steiner, *Pflüger's Arch.*, 1891.— Vialet, Thèse Paris, 1893.—Vitzou, *Arch. de Phys.*, 1893 et 1897.

Pupillary reaction.—E. Hesse, *Pflüger's Arch.*, LII.—E. Leyden, *Deutsche med. Wochenschr.*, 1892.—Massaut, *Arch. f. Psych.*, XXVIII, 1896.—Mendel, *Berliner klin. Wochensch.*, Nov. 1889.

Auditory innervation — sense of hearing ; internal ear.— Beauregard et Dupuy, Variation électriq. nerf acoustique excité par le son, *C. R. Ac. sc.*, 1896.—Berthelot, Sensat. acoust. par sels de quinine, *C. R. Ac. sc.*, 1890.—Bonnafont, Phén. nerv. par

pression membr. tymp., *C. R. Ac. sc.*, 1882.—Deganello, Ablat. can. demicircul. dégénérat. bulbe et cervelet, *Arch. ital. biol.*, 1899.—Dixon, Temps de réaction. *Journ. of Phys.*, 1896.—Gaglio, Anesthésie can. demi-circul., *Arch. ital. biol.* 1899.—Vulpian, Troubles par excit. app. auditif, *C. R. Ac. sc.*, 1883.—Wreden, Electr. reiz. ed Gehörorgans, *Arch. de Pflüger*, 1872.

Sense of space.—Bonnier, Physiol. du nerf de l'espace, *C. R. Ac. sc.*, 1891 ; Vertige, *Biblioth. Charcot-Debove ;* Oreille, *Encycl. aide-mémoire.*—De Cyon, Rapport nerf acoustiq. et app. mot. de l'œil, *C. R. Ac. sc.*, 1876 ; Org. périph. du sens de l'espace, *Ibid.*, 1877 ; Bogengänge und Raumsinn, *Arch. f. Anat. u. Phys.*, 1897 ; sens espace, *C. R. Ac. sc.*, 1900.—Fred. Lee, Equilib. in Fisher, *Journ. of Phys.*, 1894, 1895.

Cortical centre of audition.—Bechterew, Gehörcentra, *Arch. f. Anat. u Phys.*, 1899, suppl.

Pure verbal deafness.—Dejerine et Sérieux, *Biol.* 1897.—*Ideation ;* language.—G. Ballet, Lang, intérieur.—Binet, Altérations de la personnalité.—Egger, Lang. intérieur.—Grasset, Études cliniques.—Janet, Automatisme psychologique.—Taine, De l'intelligence.

Aphasia.—Broca . . . Siège faculté du langage, *Soc. anat.*, 1861, 2me série, p. 330, *Soc. anthropol.*, harcot 1863.—C, *Progrès médical*, 1883, pp. 23, 27, 521, 859.—Grasset, Études cliniques.—Miraillè, Th. Paris, 1896.—Wernicke, *Arbeit. ans psych. Klin. Breslau*, Heft II, Leipzig, 1895, et Grundrisse der Psychiatrie in Klin. Vorlesung, t. I, 1894.

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